A revision of the Afrotropical mole-crickets (Orthoptera: Gryllotalpidae)

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Synopsis

The 12 Afrotropical species of Gryllotalpidae, all members of *Gryllotalpa*, are revised, with six new species, one new synonymy, and one species revalidated. The songs of five of these species, and that of an Oriental species, are described for the first time. Keys are provided to the two subfamilies and five genera of Gryllotalpidae. *Gryllotalpa minuta* Burmeister, previously thought to occur in Africa, is shown to be absent there.

Introduction

The Gryllotalpidae, or mole-crickets, occur throughout the tropical and warmer temperate regions of the world. They are closely related to the Gryllidae, the true crickets, from which they differ mainly in being highly specialised for a subterranean existence. The fore legs are modified for digging, and bear two to four strongly sclerotised dactyls, and the body is covered in a dense mat of hair. Mole-crickets dig a complex of burrows within which they live, feed, sing, mate and breed, and which includes a nest chamber and a special singing burrow. They fly only rarely, usually to search for a mate. Specimens are most commonly taken at night during such flights, and often a high proportion of those so captured are females. The diet of mole-crickets varies according to the species (Matheny, 1981); they may be mainly carnivorous, mainly vegetarian or truly omnivorous. The life cycles of all the African species are totally unknown.

Several species of *Gryllotalpa*, in common with those of other gryllotalpid genera, become serious crop pests when occurring in large numbers (see, for example, Vayssière & Mimeur, 1925). Even species which are principally carnivorous can cause extensive mechanical damage to crops by their burrowing activities (Matheny, 1981). Mole-crickets have been reported as damaging tobacco, rice, sugar cane, potatoes and other crops, as well as lawns, seed beds and ornamental plants. Since most of the common African, Asian and Australian species have

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previously been lumped together under the name '*Gryllotalpa africana*', it is usually this species which is blamed for the damage. However, this study has shown that true *africana* does not occur outside Africa, and even in Africa it is likely that other species also cause damage. Since different species seem to require different soil conditions, particularly with respect to moisture content (Bennet-Clark, 1970), it is likely that crops requiring different soil conditions will be affected by different species. For example, a species occurring in very wet conditions might be found damaging rice crops, but is unlikely to affect potatoes. It is hoped that the present study will facilitate investigation of the relative economic importance of the various species.

Material

In addition to material in the British Museum (Natural History), I have examined specimens from a number of other depositories, through the kindness of the specialists mentioned. The most important and numerous were from the Musée Royal de l'Afrique Centrale, Tervuren. The depositories from which I have seen material are listed below, together with the abbreviations I have used for them.

ANS	Academy of Natural Sciences of Philadelphia, U.S.A.
BMNH	British Museum (Natural History), London, England
IAR	Institute of Agricultural Research, Samaru, Nigeria
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MNH	Muséum d'Histoire Naturelle, Geneva, Switzerland
MLU	Martin-Luther-Universität, Halle, East Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
MZSUS	Museo Zoologico della Specola, Università degli Studi, Florence, Italy
NM	Naturhistorisches Museum, Vienna, Austria
NMK	National Museum of Kenya, Nairobi, Kenya
SAM	South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa
UZM	Zoologisk Museum, Copenhagen, Denmark
ZL	Zoologisk Laboratorium, Aarhus University, Aarhus, Denmark

I have examined the types of all the described species except those of *minor* and *africana*, which must be considered lost. The type-series of *minor* is in neither the MNHU, nor the ZM, between which the collection containing it was divided; and that of *africana* is not in the MNHN where Palisot de Beauvois' collection is deposited.

I have also examined seven specimens labelled as syntypes of *G. orientalis* Burmeister: two males and two females from the MLU, and one male and two females from the MNHU. Of these, only the three from the MNHU have data agreeing with the original description. I am here designating as LECTOTYPE the male, which was originally from The Tranquebar Museum and was collected in Manila, Philippines.

Taxonomic characters

The main characters used here for distinguishing between species are the male stridulatory file and the venation of the male fore wing. The male genitalia, which are usually a valuable character in the Gryllidae, are less useful in the African *Gryllotalpa*, except for the characteristic genitalia of *africana*. The females are largely indeterminable, and no key to them is given, although those of some species can be recognised with practice.

The shape and length of the dactyls of the fore tibiae, often used in the past, do not provide reliable taxonomic characters. Although they show some variation between species, the dactyls evidently wear down considerably with use.

The stridulatory file of the female shows great intra-specific variation, and does not appear to be useful in distinguishing between species. Although female mole-crickets are known to stridulate, the sounds they produce are not pure frequencies, and are probably not used for mate recognition.

Most African species of *Gryllotalpa* apparently occur only in the macropterous form, in which the hind wings extend well beyond the tip of the abdomen in dried specimens. However, all specimens of *microptera* and some of *debilis* are micropterous, their hind wings being shorter than the abdomen, and often shorter than the fore wings.

Methods

The stridulatory file was examined directly using a binocular microscope. It was exposed by raising the uppermost fore wing, usually the right one, after relaxing it with a few drops of 10% ammonia solution to which a little detergent had been added. Drawings of the file were prepared, using a microprojector, from replicas made using the method described by Ragge (1969: 172) for Tettigoniidae. The terminology used for the wing venation is that of Ragge (1955).

All drawings other than those of the stridulatory files were made using a Wild M5 microscope and camera lucida. Brief diagnoses of previously described species are given, and all new species are described in full.

Genitalia preparations were made in the following way. The tip of the abdomen was relaxed using a drop or two of distilled water, together with steam from a water bath. A longitudinal mid-ventral incision was made along the last three or four abdominal sternites. The viscera were removed and cleared in cold 20% KOH, and rinsed several times in distilled water. The genitalia were separated out, and eventually preserved in a tube of glycerine pinned underneath the specimen.

For identification purposes, the characteristic long ventral processes of *africana* (Figs 3, 4) may be exposed in situ, after the tip of the abdomen has been relaxed, by pulling back the subgenital plate and the covering membrane. The term 'ventral process' is used in the absence of established terminology for gryllotalpid genitalia or any clear homology with parts of gryllid genitalia.

The term 'stridulatory area' is used for the pair of large cells of the male fore wing, the anterior of which is the harp.

The dimensions of the stridulatory area and stridulatory file were measured using a Vickers Steros II microscope with eyepiece graticule. The length of the stridulatory area was taken to be equal to the length of the harp, and the width of the area was measured at its maximum.

All other measurements were made using vernier callipers. The body length was measured from the front of the head to the tip of the abdomen. This measurement is influenced both by the attitude of the head and by the degree of shrinkage of the abdomen in drying, and is therefore less reliable than the other measurements given. In most cases, 50 males and 50 females of each species were measured, where these were available. All measurements are given in millimetres.

The oscillograms shown in Figs 52–63 were made using a Mingograf 34T. The following acoustic terms are used in song descriptions. A syllable is the sound produced by a single wing stroke, and an echeme is a discrete group of syllables. The syllable repetition rate is the number of syllables per unit time, and in complex songs it is measured within a single echeme. The echeme repetition rate is the number of echemes per unit time. These definitions are those of Broughton (1964; 1976), and are illustrated in Fig. 52. The carrier frequency is the frequency within each syllable, and is probably equal to the tooth impact rate (Sismondo, 1979). This is the frequency of the musical note heard.

Information on distributions is based entirely on specimens studied. Previously published records are considered unreliable. The term 'Afrotropical Region' is used here but excludes the Malagasy Region, and many of the offshore islands are not specifically treated due to lack of material.

My approach is entirely phenetic, with no attempt to trace any possible phylogenetic relationships.

GRYLLOTALPIDAE Leach

Gryllotalpida Leach, 1815: 119. Type-genus: *Gryllotalpa* Latreille.
Scariphasteae Fieber, 1851: 17. [Not based on the name of a contained genus and therefore unavailable under Article 11(e) of the *International Code of Zoological Nomenclature.*]
Gryllotalpina; Fieber, 1852: 6.
Gryllotalpiens; Saussure, 1874: 333.
Gryllotalpites; Saussure, 1874: 334.
Gryllotalpidae; Lopez-Seoane, 1878: 375.
Gryllotalpinae; Saussure, 1894: 199.
Gryllotalpini; Redtenbacher, 1900: 140.
Curtillinae 'A'; Kirby, 1906: 1. Type-genus: *Curtilla* Oken.
Curtillidae; Bruner, 1915: 259.
Gryllotalpoidea; Karny, 1907: 32.

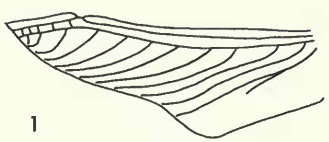
♂ ♀. Head with two ocelli and two compound eyes. Fore legs highly modified for digging, tibiae bearing two to four dactyls. Male fore wings lacking mirror. Ovipositor absent.

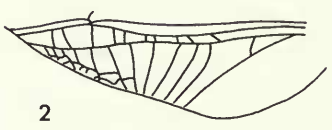
Discussion. The Gryllotalpidae consist of five easily recognisable genera. Two of these, *Neocurtilla* and *Gryllotalpella*, are restricted to the New World. One mainly New World genus, *Scapteriscus*, has two representatives in the Oriental region. The remarkable genus *Triamescaptor* contains a single, wholly apterous species found only in New Zealand. All the remaining species belong to the largest, entirely Old World genus *Gryllotalpa*.

Although the Gryllotalpidae have not usually been subdivided, some authors (Zeuner, 1939; Ragge, 1955; Vickery, 1977) have recognised two subfamilies, placing *Scapteriscus* in its own subfamily, Scapteriscinae, and leaving the remaining four genera in the Gryllotalpinae. This division is based on a difference in the origin of the basal spur of the fore leg, which arises from the trochanter in *Scapteriscus*, and from the femur in the other genera; I consider this division to be justified, and in the key to genera the two subfamilies are separated accordingly.

No major revisionary work on the African species has previously been undertaken. Scudder (1869) attempted a world revision of the group, but was apparently in possession of only three African specimens. Chopard (1968) recognised seven species from Africa. In the present revision, the number of known species is increased to twelve, of which six are new, and one new specific synonym is established. All species are placed in *Gryllotalpa*.

Kirby (1906) and Chopard (1955; 1968) placed the Old World *Gryllotalpa devia* Saussure and *Curtilla madecassa* Chopard in the otherwise New World genus *Neocurtilla*, because of the lack of spines on their hind tibiae. However, the armature of the hind tibiae is highly variable, and is generally an extremely unreliable character at specific, let alone generic, level. The main difference between *Gryllotalpa* and *Neocurtilla* is the orientation of the veins of the lateral field of the fore wing (Figs 1, 2), and both species have the *Gryllotalpa* condition. *G. madecassa* **comb. n.** is endemic to Madagascar, and as such is not included in this study. In size and wing venation it is more like the European *G. gryllotalpa* (L.) than any of the African species. *G. devia* is dealt with fully in the text.

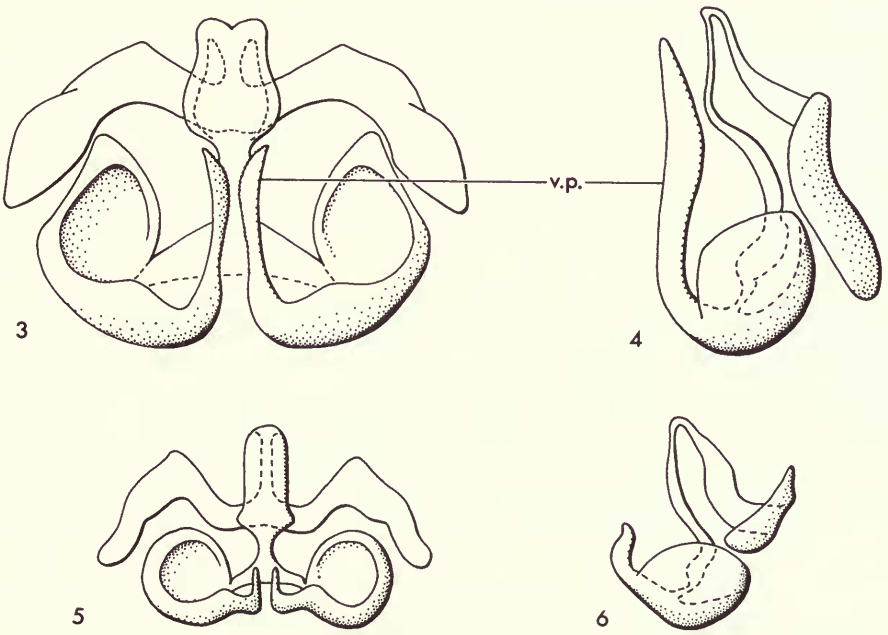




Figs 1, 2 Lateral field of right male fore wing of (1) *Gryllotalpa africana*, (2) *Neocurtilla hexadactyla*.

Key to the subfamilies and genera

1 Basal spur of fore leg arising from femur; fore tibia with 3 or 4 dactyls (Gryllotalpinae) 2
– Basal spur of fore leg arising from trochanter; fore tibia with 2 dactyls. New World & India (Scapteriscinae) ..... ***SCAPTERISCUS*** Scudder
2 Fore tibia with 4 dactyls; fore and hind wings present in both sexes 3
– Fore tibia with 3 dactyls; both sexes apterous. New Zealand ..... ***TRIAMESCAPTOR*** Tindale
3 Fore tibia with covered tympanum, opening in the form of a slit; stout-bodied insects 4
– Fore tibia with exposed tympanum; slender, delicate insects. South America ***GRYLLOTALPELLA*** Rehn
4 Veins of lateral field of fore wing as in Fig. 1, all pointing towards wing-tip. Old World ***GRYLLOTALPA*** Latreille
– Veins of lateral field of fore wing as in Fig. 2, the more distal ones pointing towards the wing-base. New World..... ***NEOCURTILLA*** Kirby



Figs 3–6 Male genitalia of (3) *Gryllotalpa africana*, ventral view, (4) *G. africana*, lateral view, (5) *G. robusta*, ventral view and (6) *G. robusta*, lateral view. v.p. = ventral process.

GRYLLOTALPA Latreille

Gryllotalpa Latreille, 1802: 275. Type-species: *Gryllus Acheta gryllotalpa* Linnaeus, by monotypy.
Curtilla Oken, 1815: 445. Type-species: *Gryllus Acheta gryllotalpa* Linnaeus, by monotypy.
Austrotalpa Mjöberg, 1913: 30. Type-species: *Austrotalpa pluvialis* Mjöberg [= *Gryllotalpa nitidula* Serville], by monotypy. [Synonymised by Tindale, 1928: 4.]

♂ ♀. Fore tibiae with four dactyls. Tympana covered, opening in the form of a slit. Basal spur of fore leg arising from femur. Fore and hind wings present. Veins of lateral field of fore wings all pointing towards wing-tips.

Discussion. The African species of *Gryllotalpa* fall into two quite distinct groups. In male fore wings of the *africana*-group, comprising *africana, bulla, debilis, devia, robusta* and *rufescens*, the stridulatory teeth are much more widely spaced at the centre of the file than at its extremities, and the radius is divided distally into two branches. In male fore wings of the *parva*-group, comprising *brevilyra, elegans, microptera, parva, pluridens* and *spissidens*, the stridulatory teeth are more or less evenly spaced, and the radius is undivided. These characters are constant in all

species except *rufescens*, and possibly *devia*, in which the form of the radius is somewhat variable; these two species are placed in the first group on the basis of their stridulatory files. The form of the radius of the females is similar to that of the males, but is rather inconsistent, and is not a reliable character for identification purposes.

The species of *africana*-group are separated by a variety of male characters, as indicated in the key; those of *parva*-group chiefly by the shape of the stridulatory area. A large proportion of the females of *rufescens, spissidens* and *elegans* may be identified with practice using characters mentioned under those species, but females of the other species cannot be reliably identified. The females of *devia* and *bulla* are unknown.

DISTRIBUTION. Throughout the tropical and warmer temperate regions of the Old World.

Synonymic list of the Afrotropical species

***africana*-group**
- ***africana*** Palisot de Beauvois
  - *colini* Rochebrune
  - *confusa* Chopard **syn. n.**
  - *fossor* Scudder
- ***bulla* sp. n.**
- ***debilis*** Gerstaecker **sp. rev.**
  - *minor* Brunn
- ***devia*** Saussure **comb. rev.**
- ***robusta* sp. n.**
- ***rufescens*** Chopard

***parva*-group**
- ***brevilyra* sp. n.**
- ***elegans*** Chopard
- ***microptera*** Chopard
- ***parva* sp. n.**
- ***pluridens* sp. n.**
- ***spissidens* sp. n.**

Non-Afrotropical species of *Gryllotalpa* also covered

madecassa Chopard **comb. n.** (p. 178)
mintua Burmeister (p. 185)
orientalis Burmeister (pp. 176, 183)

Key to the Afrotropical species

Males

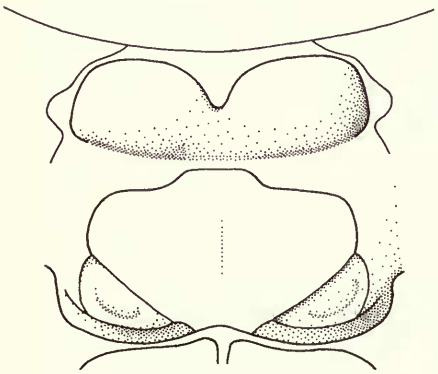
1 Stridulatory teeth much more widely spaced at centre of file than at ends (Figs 9–15). Radius of fore wing of macropterous specimens usually divided distally into R_1 and R_s (Figs 22–27) (*africana*-group) 2
– Stridulatory teeth fairly evenly spaced (Figs 16–21). Radius of fore wing of macropterous specimens never divided (Figs 29–33) (*parva*-group) 7
2 Stridulatory area very oblong (Figs 22, 23, 25–28). Mesonotum covered by pronotum and base of fore wings, scutum never enlarged (Fig. 7) 3
– Stridulatory area almost square (Fig. 24). Mesonotum usually wholly or partly exposed, scutum usually enlarged (Fig. 8) ..... ***G. bulla*** (p. 183)
3 Pronotum and legs plain brown, from light sandy-coloured to almost black, never rufous 4
– Pronotum and legs very conspicuously rufous brown 6
4 Genitalia about 3·0 mm long, with long ventral processes (Figs 3, 4) ..... ***G. africana*** (p. 182)
– Genitalia about 1·5 mm long, with short ventral processes (Figs 5, 6) 5
5 Larger, stouter species, body length 21·3–43·6 mm. Length of fore wings 10·0–13·9 mm; width of stridulatory area 2·1–3·2 mm ..... ***G. robusta*** (p. 186)
– Smaller, less stout species, body length 15·9–25·2 mm. Length of fore wings 4·4–11·0 mm; width of stridulatory area 1·0–2·2 mm ..... ***G. debilis*** (p. 184)

6 Hind tibiae with 3–5 dorsal spines. Equatorial Africa ..... ***G. rufescens*** (p. 189)
– Hind tibiae without dorsal spines. Southern Africa ..... ***G. devia*** (p. 185)
7 Fore wings not reduced, more than 7 mm long, venation as in Figs 29–33. Hind wings long, extending well beyond tip of abdomen 8
– Fore wings much reduced, less than 7 mm long, venation as in Fig. 34. Hind wings vestigial, shorter than or a little longer than fore wings ..... ***G. microptera*** (p. 193)
8 Stridulatory area not reduced, shaped as in Figs 29–31 or Fig. 33, 3·2–4·4 mm long; or if shorter, then density of teeth less than 35 per mm 9
– Stridulatory area reduced, shaped as in Fig. 32, 2·3–3·5 mm long; density of stridulatory teeth more than 35 per mm ..... ***G. brevilyra*** (p. 189)
9 Main veins and cross veins of apical field of fore wing more or less equally prominent. Stridulatory area as in Figs 29, 30 or 33 10
– Main veins of apical field of fore wing unusually prominent, cross-veins indistinct. Stridulatory area as in Fig. 30 or Fig. 31 12
10 Stridulatory file with less than 71 teeth, density of teeth 26·4–33·3 per mm. Stridulatory area as in Fig. 33 ..... ***G. parva*** (p. 195)
– Stridulatory file with more than 71 teeth, density of teeth 30·4–45·2 per mm. Stridulatory area as in Fig. 29 or Fig. 30 11
11 Stridulatory area narrower, 1·8–2·2 mm wide, shaped as in Fig. 30. West Africa & Cameroon ***G. spissidens*** (part) (p. 200)
– Stridulatory area broader, 2·1–3·0 mm wide, shaped as in Fig. 29 ..... ***G. pluridens*** (p. 197)
12 Density of stridulatory teeth less than 32 per mm. Stridulatory area as in Fig. 31. Zaire Basin ***G. elegans*** (p. 191)
– Density of stridulatory teeth more than 32 per mm. Stridulatory area as in Fig. 30. West Africa & Cameroon ..... ***G. spissidens*** (part) (p. 200)

Females

Because the most useful characters in African *Gryllotalpa* are male sexual characters, identification of isolated females is invariably difficult and usually impossible. Even the form of the radius of the fore wing, although conforming to the same general pattern as that of the male, is not consistent enough in the female to provide a reliable character. Females of some species, however, may be recognised by a variety of non-sexual characters.

The female of *rufescens* can be recognised by its very conspicuous rufous-brown coloration (see couplet 3 of key to males). In addition, the fore wings are unusually long, often reaching the



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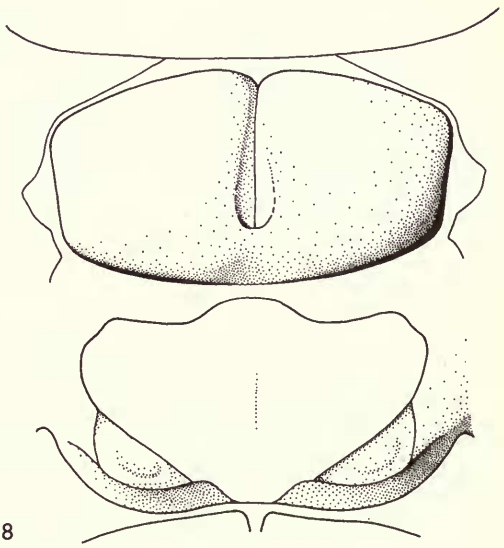

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Figs 7, 8 Meso- and metanotum of (7) *Gryllotalpa africana,* (8) *G. bulla.*

tip of the abdomen, with very straight and parallel veins (Fig. 37). The unknown female of *devia* is probably similar, but lacking dorsal spines on the hind tibiae.

Females of the allopatric (Fig. 50) *elegans* and *spissidens* have characteristically prominent fore wing veins on the dorsal field, with cross-veins indistinct or absent, although this character is often not well marked in *spissidens*.

Females of *microptera* and micropterous females of *debilis* have characteristically short fore and hind wings. Macropterous females of *debilis* are similar to *parva* and *brevilyra*. *africana, robusta* and *pluridens* are generally larger than these three, but are indistinguishable from each other. *pluridens* has a rather more restricted distribution than *africana* and *robusta*.

The female of *bulla* is so far unknown. If it has the same remarkable form of the metascutum as the male (Fig. 8), it should not be hard to recognise.

Descriptions of the Afrotropical species

The *africana*-group

Gryllotalpa africana Palisot de Beauvois

(Figs 1, 3, 4, 7, 15, 25, 38, 48, 55, 61)

Gryllotalpa africana Palisot de Beauvois, 1805: 229. Syntypes, Namibia (lost) (see p. 176). NEOTYPE ♂, South Africa (ANS), here designated [examined].

Gryllotalpa fossor Scudder, 1869: 21. LECTOTYPE ♂, South Africa (ANS), here designated [examined]. [Synonymised by Chopard, 1968: 450.]

Gryllotalpa colini Rochebrune, 1884: 30. LECTOTYPE ♀, Senegal (MNHN), here designated [examined]. [Synonymised by Chopard, 1968: 450.]

[*Gryllotalpa formosana* Shiraki; Chopard, 1934: 14. Misidentification.]

Gryllotalpa confusa Chopard, 1967: 776. LECTOTYPE ♂, Zaire (IRSNB), here designated [examined]. **Syn. n.**

Diagnosis. ♂. Venation of right fore-wing as in Fig. 25, R_1 and R_s separated distally. Stridulatory file of right fore wing as in Fig. 15 with 25–52 teeth (mean of 50 examined: 34·6) more widely spaced in centre of file than at ends, 11·4–20·8 per mm (mean of 50 examined: 15.6). Genitalia very large, with long ventral processes (Figs 3, 4). Song as in Figs 55, 61, a continuous thrill, mean syllable repetition rate 49·1–57·8/s, mean carrier frequency 2·1–2·4 kHz (based on 4 recordings).

♀. Right fore wing as in Fig. 38, R_1 and R_s separated distally.

Measurements

	Males	Females
Body length	(50): 22·0–35·0, mean 28·4	(50): 21·9–33·0, mean 28·3
Median length of pronotum	(50): 7·5– 9·9, mean 8·6	(50): 7·6– 9·7, mean 8·6
Length of hind femur	(50): 7·2–10·4, mean 8·6	(50): 7·0– 9·9, mean 8·5
Length of fore wing	(50): 9·6–13·9, mean 12·0	(50): 9·2–14·8, mean 11·9
Length of stridulatory area	(50): 3·9– 5·8, mean 4·9	
Width of stridulatory area	(50): 2·1– 2·7, mean 2·4	
Length of stridulatory file	(50): 1·6– 2·5, mean 2·2	

Discussion The identity of *africana* cannot be established from Beauvois' original description, which applies equally well to any African species. In the past, its identity has been far from settled, although two distinct genitalic forms have long been recognised among African specimens similar in external morphology; one is small and has short ventral processes typical of the genus (Figs 5, 6), the other is much larger and has long ventral processes (Figs 3, 4). Chopard (1939) referred to the first, typical form as *fossor* Scudder, and the second, atypical one as *africana*. Later (1967), following Saussure & Zehntner (1894), he called the typical form *africana*, and gave the atypical form a new name, *confusa*. In 1968 he synonymised *fossor* with *africana*.

However, two important facts have emerged in the course of this study. Firstly, the single species having the atypical genitalic form is by far the commonest species occurring in Africa, comprising about one-third of all the specimens examined. Secondly, the type-locality for

africana is 'Royaume Oware', apparently referring to the region of the Oware River, a seasonal river running into the Etosha Pan of northern Namibia; the only specimens I have seen from this area, from the collection of the ANS, are from the Etosha Pan itself, and have the atypical genitalic form.

For these reasons I am considering the species having the atypical form of genitalia (Figs 3, 4) to be *africana*. This preserves the traditional position of *africana* as Africa's commonest *Gryllotalpa*, ensures the greatest possible stability in the nomenclature, and is most likely to be true to Palisot de Beauvois' syntypes.

Although the specimens from the Etosha Pan are nearest to the type-locality, they are unusually small for the species (body length 22·0–27·7 mm), perhaps as a result of the hostile environment. In addition, recent research has shown that the song is often the most important single character in the Grylloidea, so that where possible type-specimens should be selected from populations from which song recordings have been made. For these reasons, I have selected as neotype a male from such a population at Howick, South Africa, in preference to the specimens from Etosha Pan.

Contrary to the belief of most previous authors, the single male syntype of *fossor*, here designated lectotype, possesses the atypical genitalic form. *fossor* is therefore a synonym of *africana*, as is *confusa*.

The difference in genitalic structure between *G. africana* and the other species may be related to a difference in copulatory behaviour (Alexander, 1962). A series of specimens in the BMNH from Nurtiti, Sudan is labelled as 'damaging potatoes'.

G. colini is included as a synonym of *africana*; the female lectotype cannot be definitely identified, but is most likely to belong to this species. The female paralectotype of *colini*, and that of *fossor*, are indeterminable.

MATERIAL EXAMINED

Gryllotalpa africana Beauvois, neotype ♂, **South Africa**: Natal, Mkuze Game Reserve, Nsumu Pan, 19.xi.1980 (*Otte*) (ANS). *Gryllotalpa fossor* Scudder, lectotype ♂, **South Africa**: Cape of Good Hope (ANS,). *Gryllotalpa colini* Rochebrune, lectotype ♀, **Senegal**: Kita, 1904 (*Mabille)* (MNHN). *Gryllotalpa confusa* Chopard, lectotype ♂, **Zaire**: Rutshuru, 16–30.x.1934 (*de Witte*) (IRSNB).

Zaire: 1 ♀, Rutshuru, 17–24.vi.1934 (*de Witte*); 1 ♂, Bitashimwa, Sesero, 17.viii.1934 (*de Witte*); 1 ♀ Kahojo, 16.ii.1934 (*de Witte*); 1 ♀, S. Bishoke, 2400 m, 8–19.ii.1935 (*de Witte*); 3 ♂, Lac Mugunga, Nzulu, 1500 m, 25.i.1934 (*de Witte*) 1 ♀, Kibati, 1700 m, 17.i.1934 (*de Witte*); 1n Camp Ruindi, 1000 m, 20–28.xi.1934 (*de Witte*); 3 ♂, 3 ♀, Lac Mugunga, Nzulu, 1500 m, 25.i.1934 (*de Witte*) (MRAC). (All paralectotypes of *Gryllotalpa confusa* Chopard.) In IRSNB unless otherwise stated.

In addition, about 600 adults from localities too numerous to list, from the following countries:
South Africa, Namibia, Zimbabwe, Mozambique, Zambia, Angola, Tanzania, Kenya, Uganda, Rwanda, Zaire, Somalia, Ethiopia, Sudan, Cameroon, Nigeria, Benin, Ghana, Liberia, Senegal, Socotra.

DISTRIBUTION (Fig. 48). Throughout the African continent, north to Egypt, Libya and Morocco, and also in the Canary Islands. Although previously thought to occur throughout the Old World tropics and sub-tropics, *africana* does not occur in Australia (Dr D. Otte, pers. comm.), and in Asia and Indonesia it is apparently replaced by *G. orientalis*, previously thought to be a synonym of *africana*. Its presence in southern Spain, Saudi Arabia and the Malagasy Region is likely, but unconfirmed.

Gryllotalpa bulla sp. n.

(Figs 8, 11, 24, 49, 53, 59)

♂. Fairly uniform brown in colour, veins of fore wings darker, slightly rufous. Pronotum not unusually large compared with head. Mesoscutum more or less exposed between pronotum and base of fore wings, often greatly enlarged (Fig. 8). Fore wings broad; venation of right fore wing as in Fig. 24; stridulatory area very broad, almost square; radius divided distally into R_1 and R_s. Stridulatory file of right fore wing as in Fig. 11, with 35–49 teeth (mean of 9 examined: 41·3) more widely spaced in centre of file than at ends, 12·9–15·2 per mm (mean of 9 examined: 14·1). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 1–4 spines on internal margin, or unarmed. Genitalia similar to *robusta* (Figs

5, 6). Song as in Figs 53, 59, a continuous trill; mean syllable repetition rate 128·5/s, mean carrier frequency 4·8 kHz (based on 1 recording).

♀ unknown.

MEASUREMENTS

	Males
Body length	(8): 27·7–32·8, mean 27·3
Median length of pronotum	(9): 7·4– 8·8, mean 8·3
Length of hind femur	(9): 6·6– 7·8, mean 7·3
Length of fore wing	(9): 11·5–13·3, mean 12·3
Length of stridulatory area	(9): 3·8– 4·5, mean 4·2
Width of stridulatory area	(9): 2·9– 3·3, mean 3·1
Length of stridulatory file	(9): 2·4– 3·5, mean 2·9

DISCUSSION. This species is remarkable in the form of the mesonotum (Fig. 8); the scutum is sometimes greatly enlarged, and this is the only species in which it is exposed. In all other species the pronotum and base of the fore wings cover the scutum.

The single male from Kenya excluded from the type-series differs in having a longer stridulatory area (6·3 mm) and fewer (23), less densely packed stridulatory teeth (6·6 per mm). This specimen may represent an extreme variant, or a separate species. A recording of the song of this form might confirm its status.

MATERIAL EXAMINED

Holotype ♂, **Tanzania**: Serengeti N.P., Seronera, 14.x.1980 (*Otte*) (ANS).

Paratypes. **Zaire**: 3 ♂, Katanga, Lubumbashi ('Elisabethville'), 1911, xi.1911, 1930 (*Buttgenbach, Miss. Agric., Lamoral*) (MRAC; BMNH); 1 ♂, Kapiri, ix.1912 (*Miss. Agric.*) (MRAC); 5 ♂, Katanga, Kasenia, 15.ix.–15.x.1930 (*de Witte*) (MRAC; BMNH).

Material excluded from the type-series. **Kenya**: 1 ♂, Masai Reserve, 7.ii.1935 (*Benson*) (UZM).

DISTRIBUTION (Fig. 49). Central and East Africa; holotype found in very wet soil.

Gryllotalpa debilis Gerstaecker **sp. rev.**

(Figs 13, 14, 27, 28, 40, 41, 48)

Gryllotalpa debilis Gerstaecker, 1869: 211. Holotype ♂, TANZANIA (MNHU) [examined]. [Synonymised with *G. minuta* by Chopard, 1968: 451.]

Gryllotalpa minor Brunn, 1901: 276. Syntypes, TANZANIA (lost) (see p. 176). NEOTYPE ♂, TANZANIA (MNHU), here designated [examined; same specimen as holotype of *G. debilis* Gerstaecker, 1869: 211]. [Synonymised with *G. minuta* by Chopard, 1968: 451.]

DIAGNOSIS. ♂. Venation of right fore wing as in Figs 27, 28, R_1 and R_s separated distally. Stridulatory file of right fore wing as in Figs 13, 14, with 21–48 teeth (mean of 50 examined: 31·5) more widely spaced in centre of file than at ends, 11·6–30·0 per mm (mean of 50 examined: 19·6). Hind wings variable, sometimes extending well beyond tip of abdomen, sometimes slightly shorter than fore wings, more often intermediate. Hind tibiae armed above with 2–4 spines on internal margin. Genitalia similar to *robusta* (Figs 5, 6).

♀. Right fore wing as in Figs 40, 41, R_1 and R_s separated distally.

MEASUREMENTS

	Males	Females
Body length	(50): 15·9–25·2, mean 20·8	(50): 19·2–26·5, mean 22·9
Median length of pronotum	(50): 5·2– 8·2, mean 6·7	(50): 6·1– 7·9, mean 7·0
Length of hind femur	(50): 5·1– 7·6, mean 6·4	(50): 5·9– 7·9, mean 6·6
Length of fore wing	(50): 4·4–11·0, mean 7·9	(50): 3·9–10·2, mean 7·9
Length of stridulatory area	(50): 2·3– 4·6, mean 3·6	
Width of stridulatory area	(50): 1·0– 2·2, mean 1·7	
Length of stridulatory file	(50): 1·2– 2·5, mean 1·6	

DISCUSSION. *G. debilis* is very similar to *robusta* (see p. 186), but is smaller and less stout. Both species show unusually wide variations in minor characters such as colour, colour pattern, size

and shape, and in the form of the stridulatory area and stridulatory file, suggesting that they may in fact be complexes of several very similar species. However, I have not been able to subdivide them satisfactorily on the basis of morphological characters.

This species has been confused with *G. minuta*, from which it differs chiefly in the smaller number of stridulatory teeth (number on holotype of *minuta*: 63). *minuta* is common in the Oriental region, but does not occur in Africa.

The type-series of *minor* was from Zanzibar, the type-locality of *debilis*, and since these two names have been associated for several years, I have decided to treat them as synonyms. In order to establish their synonymy firmly, I have designated the holotype of *debilis* as neotype of *minor*, the name *debilis* taking priority.

G. debilis is also morphologically indistinguishable from *G. orientalis*. The two may be synonymous, and if so this would apparently be the only species of *Gryllotalpa* common to the Afrotropical and Oriental regions. The two taxa are treated as specifically distinct until a recording of the song can be compared with that of *orientalis* (Figs 57, 63).

G. debilis is the only Afrotropical species of which both macropterous and micropterous forms are known. The micropterous form is superficially similar to *microptera*, but differs in the form of the stridulatory file (Figs 14, 19), and in having the radius divided distally into R_1 and R_s.

MATERIAL EXAMINED

Holotype ♂, **Tanzania**: Zanzibar (MNHU).

Zambia: 3 ♂, 5 ♀, 1n, Lake Bangweulu, Mbawala Is., x.–xi.1946 (*Steele*) (BMNH). **Namibia**: 1 ♂, Naukluft, 1300–1500 m, 7–10.xii.1933 (*Jordan*) (BMNH). **Uganda**: 1 ♂, Mwiri, Turtle Pool, 20.xi.1954 (*Corbet*) (BMNH). **Zaire**: 1 ♂, Bas-Kasai, ix.1920 (*Vanderijst*); 1 ♂, Equateur, Boende, 13.iv.1926 (*Hulstaert*); 2 ♂, Sankuru, Komi, iv.–v.1930 (*Ghesquière*); 1 ♂, Katanga, Katompe, 1–15.vi.1930 (*Gérard*); 1 ♂, Eala, 22.x.1931 (*Brédo*); 1 ♀, Ruwenzori, Mutwanga, ii.–iii.1937 (*Hackars*); 3 ♂, 1 ♀, Mutsora, 1939 (*Hackars*) (IRSNB); 1 ♂, 3 ♀, Kasika, R. Ngombe, 8–10.vi.1949 (*Laurent*); 64 ♂, 111 ♀, Upemba NP, Ganza, 8.vi.1949, 5.vii.1949 (*de Witte*) (15 ♂, 23 ♀ in BMNH); 9 ♂, 1 ♀, Garamba NP, xi.1949, 2.i.1950, 6.i.1950, 18.viii.1950, 6.x.1951, 28.xi.1951, 21.viii.1952 (*Demoulin, De Saeger*) (1 ♂ in BMNH); 1 ♂, Kwango, Popakabaka, i.1952 (*Pierquin*); 9 ♂ 12 ♀, 8 n, Albert NP, Ruwenzori Massif, near Kalonge, Kisesa, 23.v.1953 (*Vanschuytbroeck & Kekenbosch*) (3 ♂, 4 ♀, 2 nn in BMNH); 12 ♂, 4 ♀, 8 n, Albert NP, various localities, 2.iii.–23.vii.1957 (*Vanschuytbroeck*) (3 ♂ in BMNH); 3 ♂, 11 ♀, Stanley Pool, 3–10.x.1957, 7.x.1957 (*Bouillon*) (1 ♂, 2 ♀ in BMNH); 1 ♂, Mayumbe, Singa to Mbomba, T. Kipanzu, v.–vi.1958 (*Laurent*); 1 ♂, 3 ♀, Mayumbe, Vemba to Minionzi, T. Tshela, vi.–vii.1958 (*Laurent*). **Ethiopia**: 1 ♂, Adda shore of L. Hora Harsadi, 3.xii.1936 (*Omer-Cooper*) (BMNH). **Nigeria**: 1 ♂, Sokoto, 1921 (*Moiser*) (BMNH); 1 ♂, 1 ♀, Ibadan, i.–vi.1954 (*Clausen*) (UZM); 1 ♂, 8 ♀, Western Province, 3·5 miles N. of Oyo, near Idode, 16.xii.1960 (*Jago*) (BMNH); 1 ♂, Western Pronce, Ibadan, University College, 17.xii.1960 (*Jago*) (BMNH); 1 ♂, Zaria, Samaru, 1979 (*Deeming*) (IAR). **Ghana**: 1 ♂, Accra, Legon, 9.iii.1969 (*Richards*) (BMNH). **Chad**: 1 ♂, Bebedjia, xi.1965 (*Schmitz*). In MRAC unless otherwise stated.

DISTRIBUTION (Fig. 48). Tropical Africa; also known from Mauritius, Rodriguez, the Seychelles and Saudi Arabia. The record from Namibia, which is based on a single male in the BMNH, is in need of confirmation.

Gryllotalpa devia Saussure **comb. rev.**

(Figs 10, 22, 48)

Gryllotalpa devia Saussure, 1877: 25. Holotype ♂, SOUTH AFRICA (MHN) [examined].
Neocurtilla devia (Saussure) Kirby, 1906: 2.

DIAGNOSIS. ♂. Pronotum and legs rufous-brown, colour 38 (Tawny) or 40 (Cinnamon-Rufous) in Naturalist's Colour Guide (Smithie, 1975). Pronotum very large compared with head. Venation of right fore wing as in Fig. 22, radius divided distally into R_1 and R_s in holotype, possibly sometimes undivided as in *rufescens*. Stridulatory file of right fore wing as in Fig. 10, with 40 teeth, more widely spaced in centre of file than at ends, overall density 12 per mm. Hind tibiae without dorsal spines.

♀ unknown.

MEASUREMENTS

	Male holotype
Body length	35·0
Median length of pronotum	12·0
Length of hind femur	10·0
Length of fore wing	15·0
Length of stridulatory area	5·8
Width of stridulatory area	3·7
Length of stridulatory file	3·3

DISCUSSION. Kirby (1906: 2) placed this species in his New World genus *Neocurtilla*, presumably because of the absence of dorsal spines on its hind tibiae. However, this is not a reliable generic character, and the venation of the lateral field of the fore wing clearly places *devia* in *Gryllotalpa* (see p. 178). The fragile condition of the holotype prevents examination of the genitalia, but those of the only other recorded specimen have been figured by Chopard (1955: fig. 16), and do not appear to have any unusual characteristics. The orientation of some of the stridulatory teeth appears to be reversed in the holotype (Fig. 10), but this may be abnormal.

MATERIAL EXAMINED

Holotype ♂, **South Africa**: Cape of Good Hope (MHN).

DISTRIBUTION (Fig. 48). Southern Africa, known only from the Cape of Good Hope and Lesotho. Apparently associated with drier regions than is usual for mole-crickets.

Gryllotalpa robusta sp. n.

(Figs 5, 6, 12, 26, 39, 49, 54, 60)

[*Gryllotalpa africana* Palisot de Beauvois; Saussure & Zehntner, 1894: 406; Chopard, 1967: 775. Misidentifications.]

[*Gryllotalpa fossor* Scudder; Chopard, 1939: 6. Misidentification.]

♂. Fairly uniform in colour, light brown to black, veins of fore wings darker. Pronotum not unusually large compared with head. Mesoscutum not exposed, concealed by pronotum and base of fore wings, never enlarged. Venation of right fore wing as in Fig. 26; stridulatory area more or less rectangular; radius divided distally into R_1 and R_s. Stridulatory file of right fore wing as in Fig. 12, with 30–42 teeth (mean of 7 examined: 35·7) more widely spaced in centre of file than at ends, 11·0–16·0 per mm (mean of 7 examined: 12·9). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 2–4 spines on internal margin. Genitalia small, with short ventral processes (Figs 5, 6). Song as in Figs 54, 60, a continuous trill, mean syllable repetition rate 98·5/s, mean carrier frequency 1·6 kHz (based on 1 recording).

♀. Right fore wing as in Fig. 39, radius usually divided distally into R_1 and R_s.

MEASUREMENTS OF HOLOTYPE

Body length	:	35·2
Median length of pronotum	:	8·8
Length of hind femur	:	8·8
Length of fore wing	:	13·7
Length of stridulatory area	:	6·0
Width of stridulatory area	:	3·0
Length of stridulatory file	:	2·9

OVERALL MEASUREMENTS

Body length	(50): 21·3–35·2, mean 26·3	(11): 23·4–35·1, mean 29·5
Median length of pronotum	(50): 7·0–10·0, mean 8·0	(11): 6·6– 8·9, mean 8·0
Length of hind femur	(50): 6·7–10·0, mean 7·9	(11): 7·0–10·0, mean 8·6
Length of fore wing	(50): 10·0–13·9, mean 11·7	(11): 10·9–13·5, mean 11·7
Length of stridulatory area	(50): 4·0– 6·1, mean 5·1	
Width of stridulatory area	(50): 2·1– 3·2, mean 2·6	
Length of stridulatory file	(50): 1·6– 3·0, mean 2·3	
Number of stridulatory teeth	(50): 17·0–42·0, mean 29·4	

Overall density of stridulatory teeth (50): 9·0–18·0, mean 13·0

Discussion. This is the most nondescript of all the African mole-crickets. It was previously confused with *africana*, and also misidentified as *fossor*, which is now a synonym of *africana*. Externally, it is indistinguishable from *africana* but lacks the characteristic male genitalia of that species (Figs 3–6) and differs radically from it in song (Figs 54, 55, 60, 61). It is also very similar to *debilis*, differing chiefly in its larger size and more robust shape.

Both *robusta* and *debilis* show a much greater range of variation in minor characters, and in the form of the stridulatory area and stridulatory file, than that normally found within a single species. These characters, such as colour, colour pattern, size and shape, appear to be quite consistent within single populations, and strongly suggest that both *robusta* and *debilis* are in fact complexes of several very similar species. However, I have been unable to subdivide them satisfactorily on the basis of the morphology.

Because of the similarities between *robusta* and *debilis* in major characters, particularly the fore wing venation and the gross form of the stridulatory file (Figs 12, 13, 14, 26, 27, 28), and because of the great variation within both taxa, a number of specimens cannot be definitely identified as one or the other. The changes in nomenclature adopted in this paper, which leave the present species without a name, offer an opportunity simply to treat the two taxa as a single species, under the name *debilis*. However, I have decided against this for the following reasons.

1. Such a step would involve combining two taxa previously recognised as separate. This would be misleading, in view of the evidence suggesting that there are more than two species, not less.

2. *debilis* is more similar to *orientalis* than to *robusta*, but *orientalis* and *robusta* have different songs (Figs 54, 57, 60, 63). This provides further circumstantial evidence for a specific difference between *debilis* and *robusta*, though the song of *debilis* itself is unknown.

3. The holotype of *robusta* is clearly different from that of *debilis*, and its song is known. Despite the variation within each taxon, and the areas of overlap between them, the majority of specimens can be assigned to one or the other on the basis of the characters described.

Because of the great variation involved, I have not designated paratypes of *robusta*. I have given separate series of measurements for the holotype, and for all the specimens grouped under *robusta*.

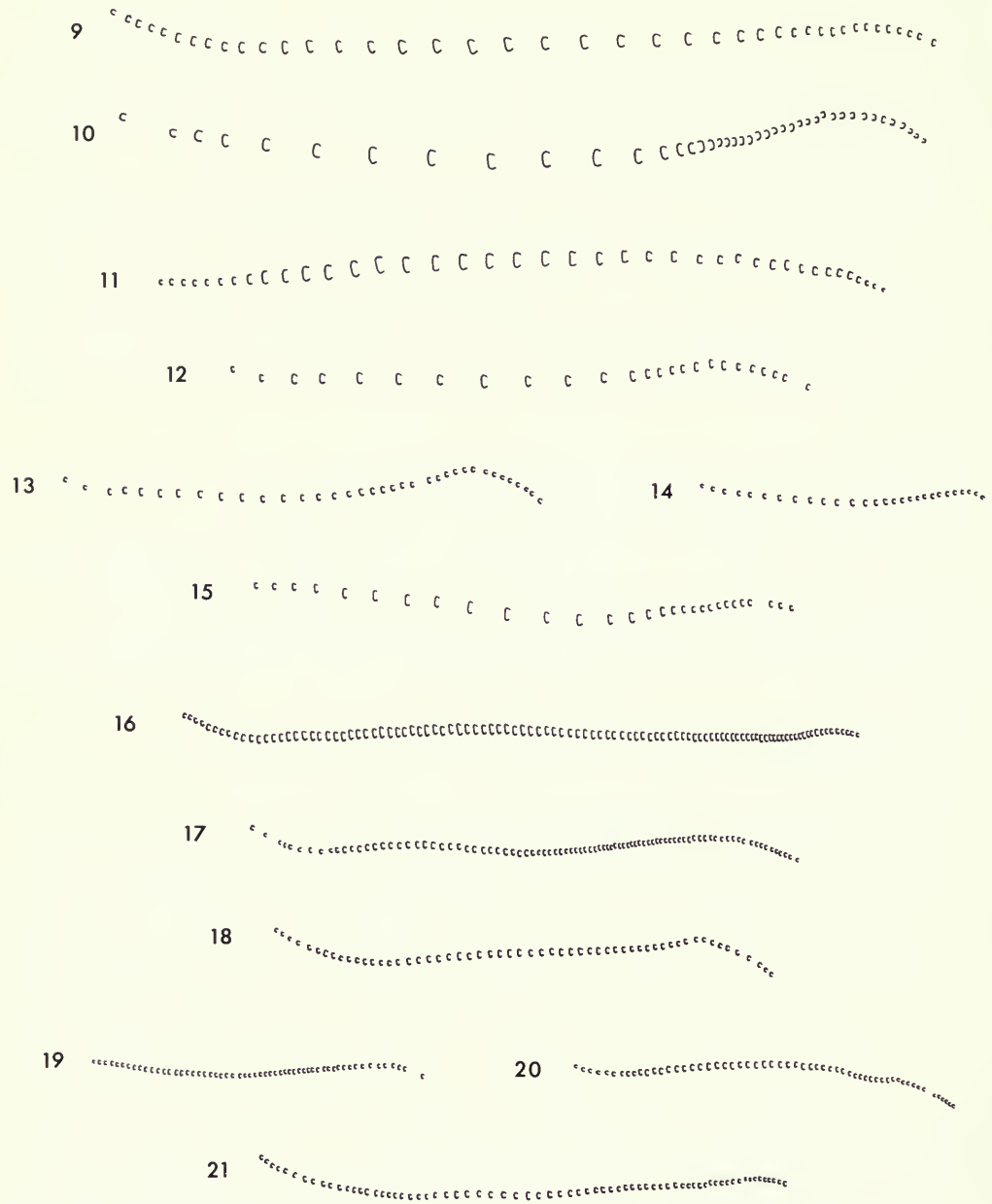
Material examined

Holotype ♂, **Tanzania**: Serengeti N.P., Musabi Plains, c. 30 miles NW. of Serona, 20.x.1980 (*Otte*) (ANS).

Material excluded from type-series. **South Africa**: 1 ♂, Kruger N.P., c. 70 miles N. of Skukuza, Olifant's Camp, 7.vii.1974 (*Pitkin*) (BMNH); **Tanzania**: 1 ♂, Ukerewe Is. (*Conrad*) (NMK); 1 ♂, Kabolo, 5.vii.1947 (*Poll*); 3 ♂, Sumbawanga, xii.1980 (*Moyer*) (BMNH). **Zambia**: 1 ♂, Lochimvar, 6–26.v.1964 (*Van Noten*). **Kenya**: 10 ♂, 1 n, Kinangop, i.1930, xi.1930 (*Turner*) (7 ♂, 1 n in NMK; 3 ♂ in BMNH); 1 ♂, Kaimosi, iii–iv.1932 (NMK); 2 ♂, 3 ♀, Lake Baringo, Molo R. mouth, 17.vi.1934 (Rehn) (2 ♂, 2 ♀ in ANS, 1 ♀ in BMNH). **Uganda**: 1 ♂, Kagora Plains, vi.1911 (*Marshall*) (BMNH); 1 ♂, Kalinzu Forest, x.1948 (*Jackson*) (NMK); 2 ♂, Mpanga Forest, Fort Portal, ii.1957 (*Carcasson*) (NMK). **Rwanda**: 1 ♂, Rubengeri, 1911 (*Lestrade*); 1 ♂, Kisenyi, i.1954 (*Bertrand*). **Zaire**: 1 ♂, Katanga; 1 ♂, Haut Congo (IRSNB); 5 ♂, Kambove, ix.1906–iii.1907 (*Neave*) (1 in BMNH); 16 ♂, Bunkeya, x.1907 (*Neave*) (3 in BMNH); 2 ♂, Kambove to Chitura, xi.1907 (*Neave*); 1 ♂, xii.1907 (*Neave*); 1 ♂, Kasenyi, 19.vii.1911 (*Stappers*); 1 ♂, Kapiri, ix.1912 (*Miss. Agric.*); 3 ♂, 1 ♀, Katanga, Mwema, vii.1927 (*Bayet*) (1 ♂ in BMNH); 1 ♂, Ituri, Butembo, xii.1928 (*Van Riel*); 1 ♂, Semliki Plain, 900–1100 m, iv.–x.1937 (*Hackars*) (IRSNB); 1 ♂, Kunungu, 1941 (*N'Kele*); 1 ♂, Bas Congo, Lemfu, x.–xii.1944 (*Beir*); 1 ♂, Kivu, Kitwabalazi, 1946 (*Herrinck*); 1 ♂, Kindia, 2.v.1948 (*Olsen*) (ZL); 5 ♂, Katanga, Kundelungu, Affl. Lualaba II, L. Moero Basin, 1680 m, 17–19.x.1951 (*Leleup*) (2 in BMNH); 9 ♂, Garamba N.P., 30.xi.1951 (*De Saeger*) (3 in BMNH); 1 ♂, L. Albert, Mahagi Port, 16.ii.1954 (*Verbeke*) (IRSNB). **Somalia**: 1 ♂, Iscia Baidoa, 12–28.vi.1978 (MZSUS). **Malawi**: 1 ♂, 2 ♀, Namalindi, 12–14.xii.1969 (BMNH). **Cameroon**: 2 ♂, 6 ♀, M'Bakaou, iii.1967 (*Chemin*) (1 ♂, 2 ♀ in BMNH); 2 ♂, 1 ♀, Koum, 20–22.i.1976. (*Puylaert*). **Ethiopia**: 6 ♂, Zegi Tsana, v.–vi.1902 (*Degen*) (BMNH). **Nigeria**: 1 ♂, 2 ♀, Zaria, Samaru, 1979 (*Deeming*) (1 ♂, 1 ♀ in IAR; 1 ♀ in BMNH). **Togo**: 1 ♂, 3 ♀, Piya, 18–22.v.1963 (*Schach*) (1 ♀ in

BMNH). **Ghana**: 1 ♂, Gold Coast (*Woodward*) (BMNH). **Sierra Leone**: 2 ♂, 2 ♀, Rokupr, 1977 (BMNH). In MRAC unless otherwise stated.

Distribution (Fig. 49). Africa south of the Sahara, and the Canary Islands. Holotype found in very wet soil.



Figs 9–21 Right male stridulatory file of (9) *Gryllotalpa rufescens*, (10) *G. devia*, (11) *G. bulla*, (12) *G. robusta*, (13) *G. debilis* (macropterous), (14) *G. debilis* (micropterous), (15) *G. africana*, (16) *G. pluridens*, (17) *G. spissidens*, (18) *G. elegans*, (19) *G. microptera*, (20) *G. brevilyra*, (21) *G. parva*.

Gryllotalpa rufescens Chopard

(Figs 9, 23, 37, 49, 52, 58)

Gryllotalpa rufescens Chopard, 1948: 110. LECTOTYPE ♂, Zaire (MRAC), here designated [examined].

Diagnosis. ♂. Pronotum and legs rufous brown, colour 38 (Tawny) or 40 (Cinnamon-Rufous) in Naturalist's Colour Guide (Smithie, 1975). Pronotum very large compared with head. Venation of right male fore wing as in Fig. 23, radius sometimes divided distally into R_1 and R_s, sometimes undivided. Stridulatory teeth of right male fore wing as in Fig. 9, with 38–68 teeth (mean of 12 examined: 51·1) more widely spaced in centre of file than at ends, overall density 9·2–18·9 per mm (mean of 12 examined: 13·1). Hind tibiae armed above with 4–5 spines on internal margin. Song as in Figs 52, 58, a continuous trill consisting of repeated echemes of three syllables; mean syllable repetition rate 80·0–100·0/s, mean echeme repetition rate 15·9–17·6/s, mean carrier frequency 2·7–2·8 kHz (based on two recordings). Genitalia similar to *robusta* (Figs 5, 6).

♀. As male except for song and genitalia, and fore wings as in Fig. 37, long, often reaching tip of abdomen, venation variable, radius sometimes divided distally into R_1 and R_s, sometimes undivided, sometimes joined with *Sc*.

Measurements

	Males	Females
Body length	(10): 25·3–32·9, mean 29·4	(4): 26·1–31·2, mean 29·0
Median length of pronotum	(12): 9·8–12·0, mean 10·7	(4): 9·6–11·2, mean 10·2
Length of hind femur	(10): 8·4–10·6, mean 9·6	(4): 9·0–10·2, mean 9·6
Length of fore wing	(12): 12·7–15·2, mean 14·0	(4): 14·5–16·6, mean 15·6
Length of stridulatory area	(12): 5·0– 6·8, mean 5·6	
Width of stridulatory area	(12): 2·9– 4·0, mean 3·2	
Length of stridulatory file	(12): 3·2– 5·1, mean 3·9	

Discussion. This species is similar to *devia*, from which it may be distinguished by the presence of spines on the dorsal surface of the hind tibiae. The song is unusual in having the syllables grouped in threes (Fig. 52).

Material examined

Lectotype ♂, **Zaire**: Kunungu, 1937 (*Nkele for Schouteden*) (MRAC).

Zaire: 1 ♂, Mongbwalu, Kilo, 1930 (*Milliau*); 1 ♂, Rutshuru, xi.1937 (*Ghesquière*); 1 ♀ (paralectotype), Mongbwalu, Kilo, vii.1938 (*Scheitz*); 1 n, Bambesa, 10.ii.1939 (*Vrydagh*); 1 ♂, Kivu, Matale, 12.v.1949 (*Marlier*); 1 ♀, Bunyakiri 1800 m, 5–7.vi.1949 (*Laurent*) (all in MRAC). **Cameroon**: 1 ♂, Metet, ii.1922 (*Lippert*); 2 ♂, Lolodorf, iv.1925, 18.xii.1926 (*Good*) (all in ANS); 1 ♂, D'Ja Posten, 1–30.vii.1936 (*Merfield*). **Uganda**: 1 ♂, near Kisoro, Busanza, 13.xii.1970 (*Bailey*); 3 ♂, 3 ♀, Kigezi, Kinanira, 22.xi.1973 (Ngirumwe) (all in BMNH).

Distribution (Fig. 49). Strictly equatorial, in moist woodland and rainforest of central Africa.

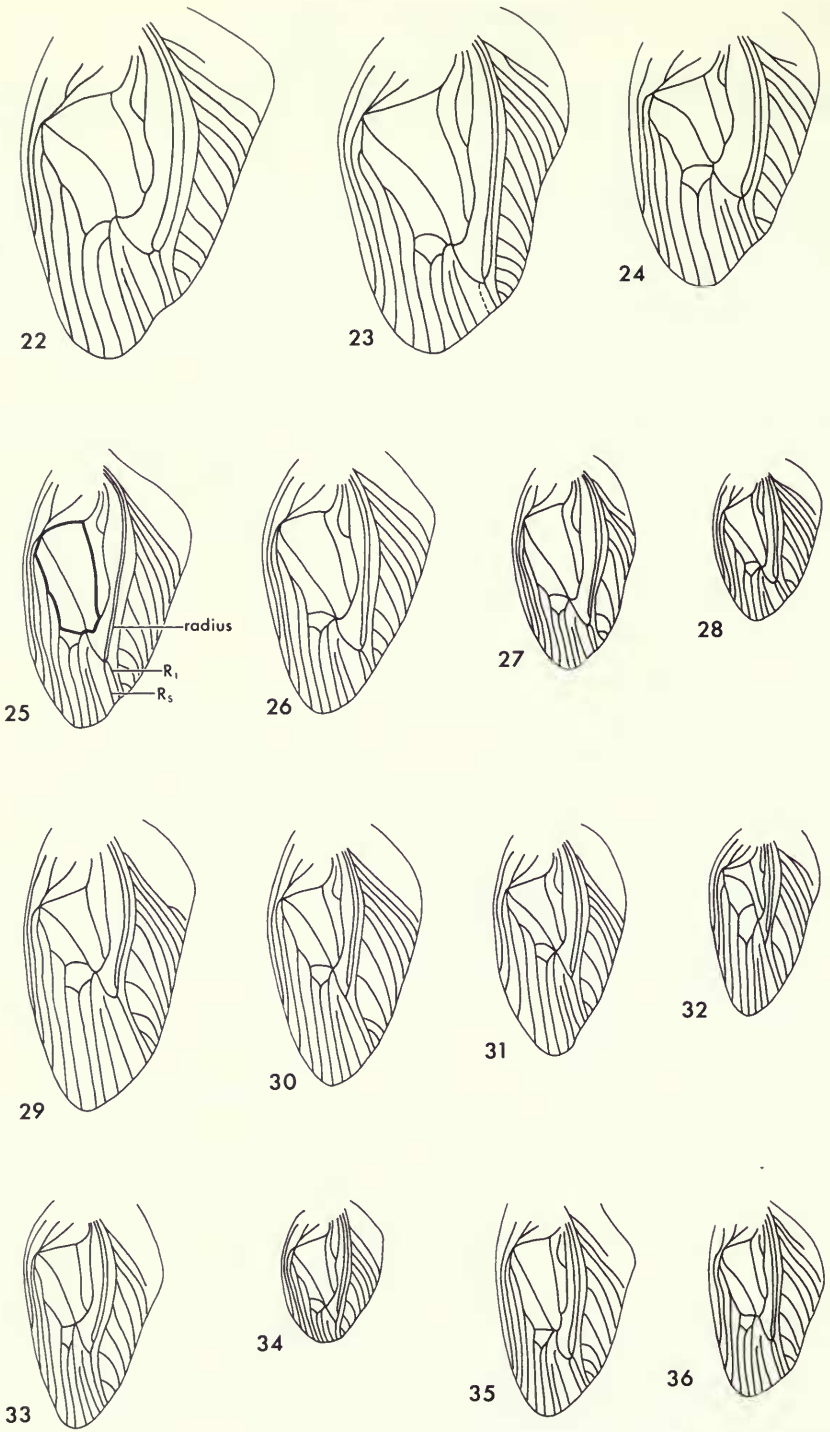
The *parva*-group

Gryllotalpa brevilyra sp. n.

(Figs 20, 32, 45, 51)

♂. Fairly uniform in colour, light to dark brown, veins of fore wings a little darker. Pronotum not unusually large compared with head. Lobes of mesonotum not exposed, concealed by pronotum and base of fore wings, never enlarged. Right fore wing as in Fig. 32; stridulatory area small, particularly posterior cell; R_1 and R_s fused; stridulatory file of right fore wing as in Fig. 20, with 51–94 teeth (mean of 50 examined: 66·6), fairly evenly spaced, 36·1–54·2 per mm (mean of 50 examined: 41·4). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 3–4 spines on internal margin. Genitalia small, with short ventral processes.

♀. Right fore wing as in Fig. 45, R_1 and R_s fused.



Figs 22–36 Right male fore wing of (22) *Gryllotalpa devia*, (23) *G. rufescens*, (24) *G. bulla*, (25) *G. africana*, showing position of radius, R_1 and R_s, and boundary of stridulatory area, (26) *G. robusta*, (27) *G. debilis* (macropterous), (28) *G. debilis* (micropterous), (29) *G. pluridens*, (30) *G. spissidens*, (31) *G. elegans*, (32) *G. brevilyra*, (33) *G. parva*, (34) *G. microptera*, (35) *G. orientalis*, (36) *G. minuta*.

MEASUREMENTS

	Males	Females
Body length	(50): 17·4–27·2, mean 22·7	(36): 17·6–30·1, mean 23·7
Median length of pronotum	(50): 5·7– 8·0, mean 7·1	(37): 5·4– 8·6, mean 6·8
Length of hind femur	(50): 5·8– 8·2, mean 7·0	(36): 5·7– 8·2, mean 6·9
Length of fore wing	(50): 7·5–11·0, mean 9·2	(37): 8·0–11·7, mean 9·6
Length of stridulatory area	(50): 2·3– 3·5, mean 2·9	
Width of stridulatory area	(50): 1·3– 1·9, mean 1·5	
Length of stridulatory file	(50): 1·2– 2·5, mean 1·6	

DISCUSSION. *G. brevilyra* may be identified by the characteristic shape of the male stridulatory area (Fig. 32). The male stridulatory file is somewhat intermediate between those of *elegans* and *parva*.

MATERIAL EXAMINED

Holotype ♂. **Nigeria**: Jos, 1968 (*Bot-Gwong*) (MRAC).

Paratypes. **Nigeria**: 2 ♂, 6 ♀, same data as holotype (1 ♂, 1 ♀ in BMNH); 2 ♂, Zaria, Samaru, 1979 (*Deeming*) (1 in IAR; 1 in BMNH). **Zaire**: 1 ♂, 1 ♀, Wenga Ifomi (*Quineaux*) (1 ♀ in IRSNB, 1 ♂ in BMNH); 1 ♂, Haut Congo (IRSNB); 1 ♂, Kwango (IRSNB); 1 ♂, Kabinda (*Muller*) (IRSNB); 1 ♂, Kikwit (*de Caters*) (IRSNB); 1 ♂, Camp Lukula, 1911 (*Daniel*); 1 ♂, Mobwasa, ix.1911 (*Giorgi*); 1 ♀, Eala, iii.1917 (*Mayne*); 2 ♂, Kikwit, 1920 (*Vanderijst*) (1 in BMNH); 1 ♂, Haut-Uelé, Moto, 1920 (*Burgeon*); 1 ♂, 1 ♀, Kisantu, 1927 (*Vanderijst*) (1 ♀ in BMNH); 2 ♂, Kisangani ('Stanleyville'), xi.1929, 1949 (*Collart, Miller*); 6 ♂, Kasai, Tshikapa, 1930 (*Fourche*) (3 in BMNH); 1 ♂, Sankuru, Komi, v.1930 (*Ghesquière*); 1 ♂, Kinshasa ('Leopoldville'), 31.viii.1930 (*de Witte*); 1 ♂, Katanga, Kakyelo, 1–9.xi.1930 (*de Witte*); 1 ♂, Kunungu, 1932 (*Nkele for Schouteden*); 1 ♂, Lomami, Kaniama, iii.–iv.1932 (*Massart*); 2 ♂, 7 ♀, Eala, v.1921, 4.xi.1930, iv.1932, 17.iv.1932, 30.viii.1933, i.1935, ix.1935, xi.1936 (*Ghesquière, Bredo, Corbisier*) (2 ♀ in BMNH); 1 ♀, Lualua, Kapanga, 1934 (*Overlaet*); 1 ♂, Katanga, Tshipama, 1936 (*Drion*); 1 ♂, Mpese, 21–26.ix.1936 (*Cooreman*) (IRSNB); 1 ♂, Kunungu, 1938 (*Nkele for Schouteden*); 1 ♀, Lubunday, Albertville, 25.vii.1938 (*Pojer*) (IRSNB); 1 ♂, N. Rosso Norma, Lake Tumba, 31.vii.1938 (*Loreux*) (IRSNB); 1 ♂, Katanga, Mukabe to Kasavi, 1939 (*De Donckere*); 1 ♂, Lokandu, iii.1939 (*Maree*); 1 ♂, Mongbwalu, v.1939 (*Lepersonne*); 1 ♂, Lubunday, Albertville, 2.vii.1939 (*Pojer*) (IRSNB, Brussels); 1 ♂, Lisala, ix.–x.1939 (*Leontovitch*); 3 ♂, Mayidi, 1942, 1945 (*Van Eyen*); 5 ♂, Lemfu, x.–xii.1945, xii.1945 (*De Beir*); 1 ♂, Tshuapua, Flandria, 1946 (*Hulstaert*); 13 ♂, 18 ♀, 1 n, Upemba N.P., various localities, 4–24.xi.1947, 6.ix–16.x.1948, 10.vi.–7.vii.1949 (*de Witte*) (3 ♂, 6 ♀ in BMNH); 1 ♂, Titule, ix.–x.1949 (*Verbeke*) (IRSNB); 1 ♂, 1 ♀, Gandajika, 27.xi.1950 (*de Francquen*)1 ♂, 1 ♀, Maniema, Mobanga, 1952 (*Henrard*); 4 ♂, 12 ♀, Bokuma, i.–ii.1952, ii.1952, iii.1952, iv.1952, vii.1952, 1953, 1954, 1955 (*Lootens*) (1 ♂ in BMNH) 1 ♂, 2 ♀, Kalina, Kinshasa ('Leopoldville'), 1952 (*Theunissen*); 2 ♂, Lake Tanganyika, Albertville, 14.viii.1953 (*Verbeke*) (IRSNB; BMNH); 1 ♂, Bokalakala, Bolobo, 1954 (*Eloy*); 1 ♂, Albert N.P., Ruwenzori Mts., Kombo, 1550 m, 19.vii.1954 (*Vanschuytbroeck & Synave*); 1 ♂, Albertville, xi.1954 (*Bomans*); 1 ♀, Bokuma, 1955 (*Lootens*); 1 ♂, Tshuapua, Ikela, 1955 (*Lootens*); 1 ♂, Mt. Hoyo, near Kivu, iv.–v.1955 (*Hostie*) (IRSNB); 1 ♂, Sankuru, Djeka, 1955–1956 (*Roiseaux*); 1 ♂, Katanga, Busumba, viii.–ix.1957 (*de Caters*); 1 ♂, Kasongo, ix.1959 (*Benoit*). **Tanzania**: 1 ♂, L. Malawi, Mbamba Bay, 12–16.iv.1936 (*Zerny*) (NM). **Zimbabwe**: 1 ♂, Balla Balla, 30.xi.1913 (*Jones*) (BMNH). In MRAC unless otherwise stated.

DISTRIBUTION (Fig. 51). This species occurs mainly in the central African rainforest, spreading west as far as Nigeria, east to Lake Victoria, and south into Zambia. The record for Zimbabwe is based on a single male in the BMNH, and is in need of confirmation.

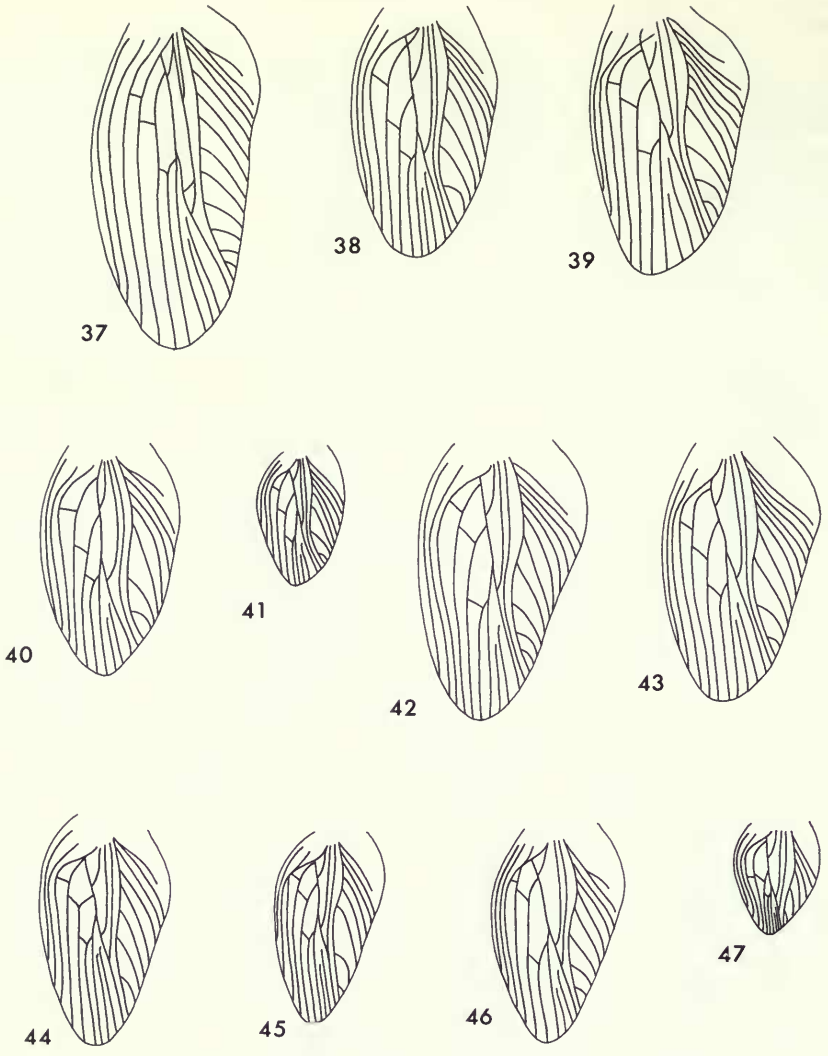
Gryllotalpa elegans Chopard

(Figs 18, 31, 44, 50)

Gryllotalpa elegans Chopard, 1934: 14. LECTOTYPE ♂, ZAIRE (MRAC), here designated [examined].

DIAGNOSIS. ♂. Venation of right fore wing as in Fig. 31, main veins unusually prominent, cross-veins indistinct or absent; R_1 and R_s fused; stridulatory area somewhat triangular, narrowing posteriorly. Stridulatory file of right fore wing as in Fig. 18, with 44–74 teeth (mean of 22 examined: 59·2) fairly evenly spaced, 23·5–31·0 per mm (mean of 22 examined: 27·2).

♀. Venation of right fore wing as in Fig. 44, main veins unusually prominent, cross-veins indistinct or absent; R_1 and R_s fused.



Figs 37–47 Right female fore wing of (37) *Gryllotalpa rufescens*, (38) *G. africana*, (39) *G. robusta*, (40) *G. debilis* (macropterous), (41) *G. debilis* (micropterous), *(42) G. pluridens*, (43) *G. spissidens*, (44) *G. elegans*, (45) *G. brevilyra*, (46) *G. parva*, (47) *G. microptera*.

MEASUREMENTS

	Males	Females
Body length	(17): 19·3–28·5, mean 23·1	(11): 21·7–27·8, mean 23·9
Median length of pronotum	(17): 6·5– 8·5, mean 7·3	(11): 6·9– 8·3, mean 7·5
Length of hind femur	(17): 6·1– 7·7, mean 6·9	(11): 6·7– 7·9, mean 7·2
Length of fore wing	(17): 8·0–10·8, mean 9·6	(11): 8·0–11·1, mean 9·7
Length of stridulatory area	(17): 2·8– 3·5, mean 3·2	
Width of stridulatory area	(17): 1·4– 1·9, mean 1·7	
Length of stridulatory file	(22): 1·6– 2·7, mean 2·2	

DISCUSSION. This distinctive species is recognisable by its prominent fore wing veins. The shape of the stridulatory area is rather similar to that of *spissidens*, but its fewer, less densely arranged

stridulatory teeth distinguish it from that species. The distribution of *spissidens* is quite different (see below).

MATERIAL EXAMINED

Lectotype ♂, **Zaire**: Bas-Congo, Yumbi, 1.x.1929 (*Bredo*)

Zaire: 1 ♀ (paralectotype) same data as lectotype; 1 ♀, L. Leopold II (*Hollebeke*); 2 ♂, Kinshasa, 13.x.1896 (*Waelbroeck*) (IRSNB); 1 ♀, Congo R., Mongala, 22.xii.1919 (*Tinant*); 1 ♀, Luebo to Luluabourg, 1921 (*Ghesquière*); 2 ♂, Bas-Congo, Yumbi, 1.x.1929 (*Bredo, Fini*) (1 in BMNH); 1 ♂, Eala, xi.1934 (*Ghesquière*); 1 ♀, Kunungu, 1941 (*N'Kele*); 1 ♂, Kalina, 12.xi.1942 (*Fiasse*); 3 ♂, 3 ♀, Kinshasa ('Léopoldville'), 1942, i.1947, ii.1947, 20–30.ix.1950, 15.xii.1950 (*Fiasse, Dartevelle, Jobels*) (1 ♂ in BMNH); 2 ♂, Boma, 19.xi.1952 (*Basilewsky*) (1 in BMNH); 1 ♀, Bokuma, i.–ii.1952 (*Lootens*) (BMNH); 1 ♀, Kasai, Djeka, 1954 (*Roiseaux*); 1 ♂, Ishango, vii.1954 (*Semliki*) (IRSNB); 30 ♂, 26 ♀, Tshuapua, Bamanya, x.1951, 1952, x.1952, i.1955, 1960, x.1961, xii.1961, 1968 (*Hulstaert, Sibbens-Pollet*); (4 ♂, 5 ♀, in BMNH); 1 ♂, Tshuapua, Boende, 1960 (*Sibbens-Pollet*). In MRAC unless otherwise stated.

DISTRIBUTION (Fig. 50). Restricted to the basin of the Congo River and its tributaries. In the coastal rainforest of West Africa and Cameroon it is replaced by *spissidens*.

Gryllotalpa microptera Chopard

(Figs 19, 34, 47, 51)

Gryllotalpa microptera Chopard, 1939: 6. LECTOTYPE ♂, ZAIRE (MRAC), here designated [examined].

DIAGNOSIS. ♂. Fore wings much shorter than abdomen, sometimes not extending beyond second abdominal segment in larger specimens, occasionally reaching fifth or sixth segment in smaller ones; venation of right fore wing as in Fig. 34, R_1 and R_s fused; stridulatory area somewhat triangular. Stridulatory file of right fore wing as in Fig. 19, with 40–60 teeth (mean of 20 examined: 52·5), fairly evenly spaced, 26.7–47.5 per mm (mean of 20 examined: 34·0). Hind wings vestigial, usually shorter than fore wings, sometimes a little longer.

♀. Fore wings sometimes a little longer than those of males; venation of right fore wing as in Fig. 47, R_1 and R_s fused.

MEASUREMENTS

	Males	Females
Body length	(27): 15·6–29·0, mean 20·6	(24): 15·7–29·6, mean 21·1
Median length of pronotum	(27): 5·2– 8·6, mean 7·0	(24): 5·0– 9·2, mean 7·2
Length of hind femur	(27): 5·0– 7·7, mean 6·2	(24): 5·0– 8·1, mean 6·4
Length of fore wing	(27): 3·3– 6·8, mean 4·8	(24): 3·6– 6·8, mean 5·3
Length of stridulatory area	(24): 1·8– 3·0, mean 2·4	
Width of stridulatory area	(24): 1·0– 1·7, mean 1·4	
Length of stridulatory file	(20): 1·0– 2·1, mean 1·6	

DISCUSSION. *G. microptera* is the only known Afrotropical *Gryllotalpa* which is invariably micropterous. Superficially it resembles the micropterous form of *debilis*, but differs from it in having fewer, more evenly spaced stridulatory teeth (Figs 14, 19), and in the radius being undivided.

MATERIAL EXAMINED

Lectotype ♂, **Zaire**: Rutshuru, 13.vi.1934 (*de Witte*) (MRAC).

Zaire: 2 ♀, Rutshuru, 26.xi.–16.xii.1933, 17–25.xii.1933 (*de Witte*) (IRSNB); 1 ♀, Lac Mugunga, 25.i.–3.ii.1933 (*de Witte*) (IRSNB); 3 ♂, 2 ♀, Lac Mugunga, 25.i.1934 (*de Witte*) (MRAC); 1 ♀, Bulengo, 29.i.1934 (*de Witte*) (MRAC) (all paralectotypes); 1 ♀, Katanga, Nyonga, v.1925 (*de Witte*); 1 ♂, Katanga, L. Kabamba, v.1927 (*Bayet*); 1 ♂, Katanga, Mwema, vii.1927 (*Bayet*); 1 n, L. Mugunga, 25.i.–3.ii.1933 (*de Witte*); 2 n, Rutshuru, 26.xi.–16.xii.1933, 26.xii.1933 (*de Witte*) (IRSNB); 2 n, L. Mugunga, 25.i.1934 (*de Witte*) (IRSNB); 1 ♂, 1 ♀, Niangara-Dungu, Ekibondo, R. Uelé, 28.ix.1934 (*Rehn*) (ANS); 1 ♂, Lisala, 6.x.1937 (*Leontovitch*); 2 ♂, 1 ♀, Rutshuru, x.1937 (*Ghesquière*) (1 ♂ in BMNH); 2 ♂, Lokandu, I. Biawa, vii.1939 (*Vissers*) (1 in BMNH); 1 ♀, Yangambi, 1940 (*I.N.E.A.C.*); 1 ♂, Bas-Congo, Mayidi, 1942 (*Van Eyen*); 2 ♂, 1 ♀, Upemba, N.P., Gorges de la Pelenge, 6–10.vi.1947 (*de Witte*) (1 ♂ in BMNH); 1 ♂, Upemba N.P., Kaswabilenga, 16.x.1947 (*de Witte*); 1 ♀, Upemba N.P., Kilwezi, R. Lufira, 9–14.viii.1948 (*de Witte*); 1 ♂, 2 ♀, Kivu, Matale, 8–14.v.1949 (*Laurent*) (1 ♀ in BMNH); 1 ♂, Kavuma-Costermansville, 16.vi.1949 (*Laurent*); 1 ♂, Costermansville-Nyagezi, 20.vi.1949

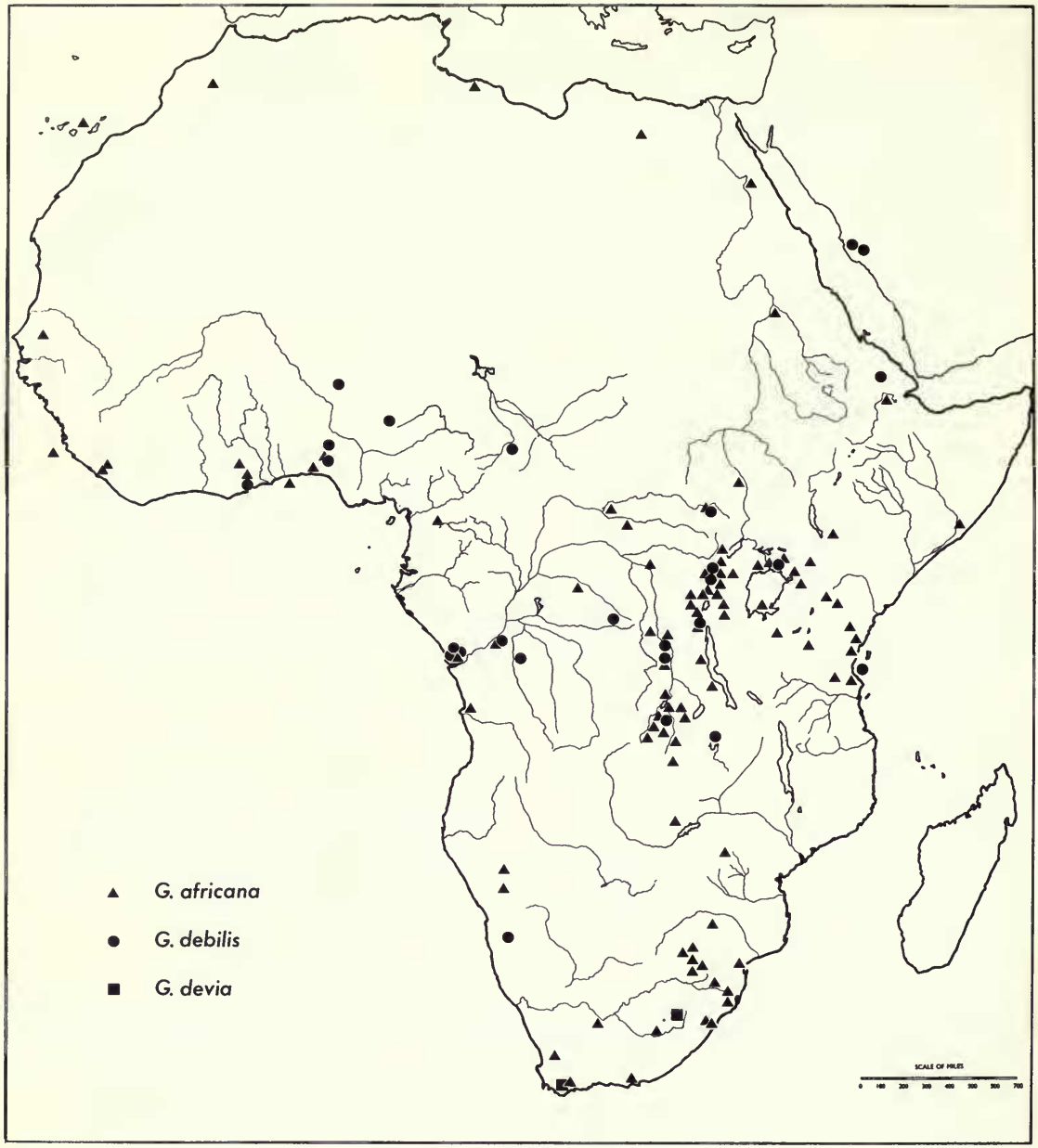


Fig. 48 Map of known distribution of *Gryllotalpa africana, G. debilis* and *G. devia*.

(*Laurent*); 1 ♀, Urundi, Kigwena, 780 m, 9.xii.1949 (*Laurent*); 1 ♂, Urundi, Kibaro, 1250 m, 15–19.xii.1949 (*Laurent*) (BMNH); 1 ♂, 1 ♀, Kivu, Kalehe Makwe, ii.1950 (*Bomans*); 9 ♂, 6 ♀, 1 n, Garamba N.P., 18.iv.1950, 30.viii.1950, 12.x.1950 (*De Saeger, Demoulin*) (2 ♂, 2 ♀ in BMNH); 1 ♀, Albert N.P., plaine Baulendu, Semliki, 21.ii.1951 (*de Wilde*); 1 ♀, Equateur, Bokuma, i.–ii.1952 (*Lootens*); 1 ♂, Albert N.P., Kibanda, Lume, 7.xii.1956 (*Vanschuytbroeck*); 1 ♂, Kivu, Uvira, Luvunyi, 5.xii.1961 (*Kiss*). **Kenya**: 1 ♀, Kakamega, xi.1976 (*Clifton*) (NMK). **Tanzania**: 1 ♂ (*Lemaire*). **Rwanda**: 3 ♀, Nyangwe, viii.–ix.1946 (*Scholl*). In MRAC unless otherwise stated.

Distribution (Fig. 51). Equatorial Africa.

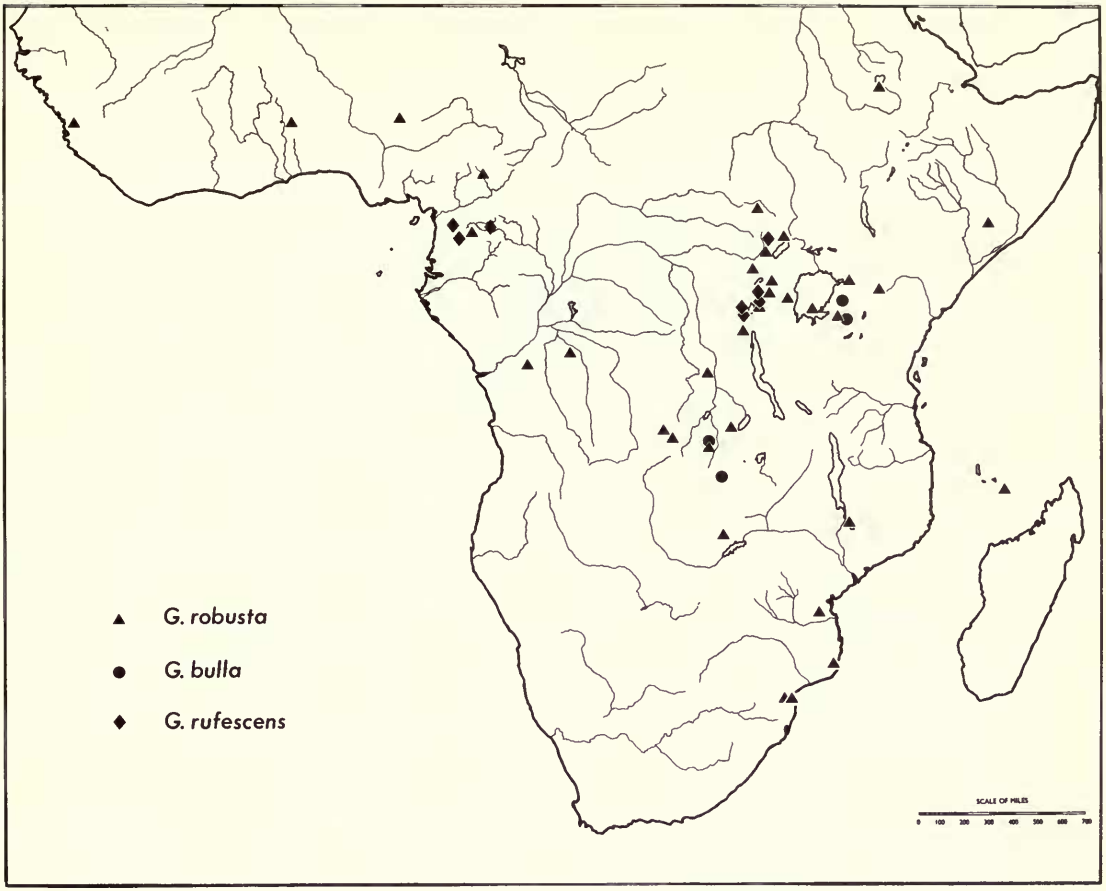


Fig. 49 Map of known distribution of *Gryllotalpa robusta, G. bulla* and *G. rufescens*.

Gryllotalpa parva sp. n.

(Figs 21, 33, 46, 50, 56, 62)

♂. Fairly uniform in colour, usually fairly light brown, veins of fore wings a little darker. Pronotum not unusually large compared with head. Lobes of metanotum not exposed, concealed by pronotum and base of fore wings, never enlarged. Right fore wing as in Fig. 33; stridulatory area fairly rectangular; R_1 and R_s fused. Stridulatory file of right fore wing as in Fig. 21, with 40–70 teeth (mean of 41 examined: 55·5), fairly evenly spaced, 26·4–33·3 per mm (mean of 41 examined: 30·0). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 2–4 spines on internal margin. Genitalia small, with short ventral processes. Song as in Figs 56, 62, a continuous trill; mean syllable repetition rate 76·4–81·4/s, mean carrier frequency 2·9–3·3 kHz (based on 2 recordings).

♀. Right fore wing as in Fig. 46, R_1 and R_s fused.

MEASUREMENTS

	Males	Females
Body length	(41): 19·3–26·0, mean 22·1	(50): 17·8–28·0, mean 22·5
Median length of pronotum	(41): 5·8– 7·7, mean 6·7	(50): 5·7– 8·3, mean 6·8
Length of hind femur	(41): 5·8– 7·7, mean 6·8	(50): 5·8– 8·5, mean 6·9
Length of fore wing	(41): 8·2–11·0, mean 9·3	(50): 7·6–12·0, mean 9·6
Length of stridulatory area	(40): 3·0– 3·7, mean 3·4	
Width of stridulatory area	(40): 1·5– 2·1, mean 1·9	
Length of stridulatory file	(41): 1·3– 2·2, mean 1·9	

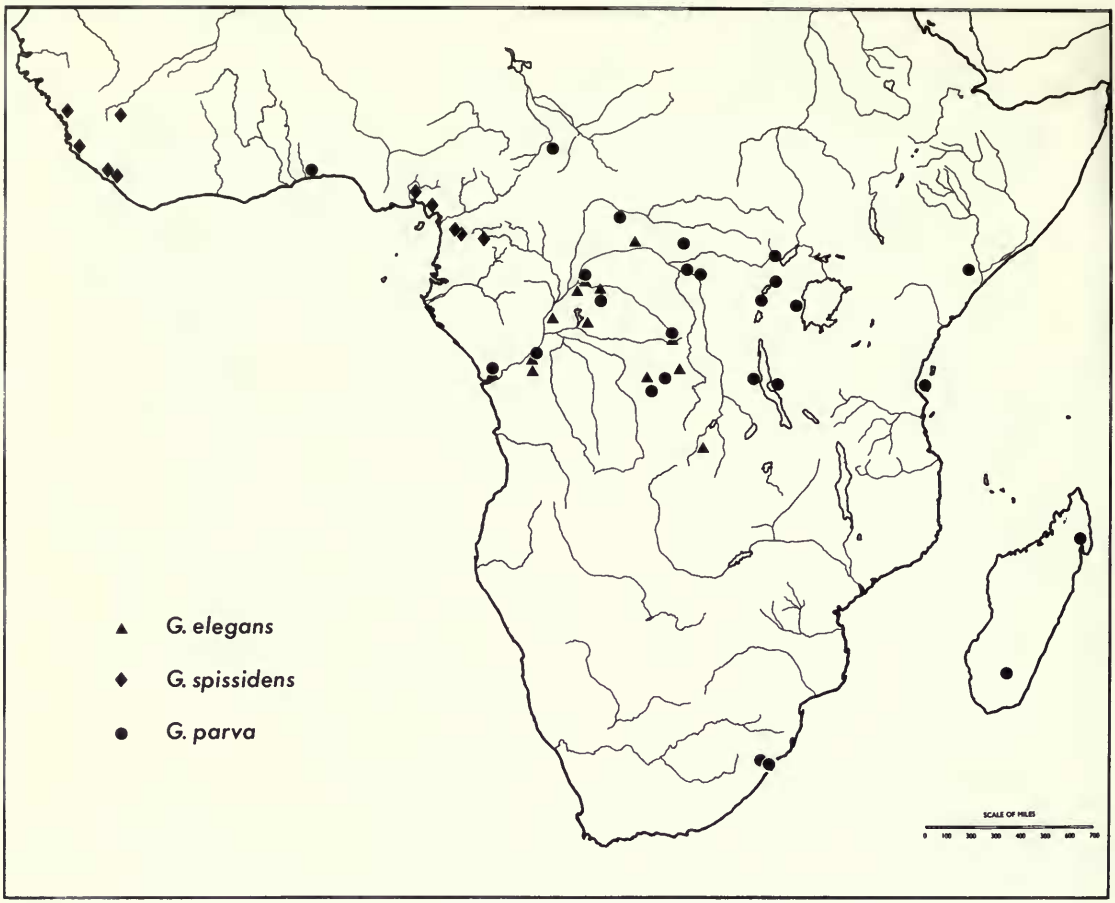


Fig. 50 Map of known distribution of *Gryllotalpa elegans, G. spissidens* and *G. parva*.

Discussion. *G. parva* is most similar to *brevilyra*, from which it may be distinguished by the shape of the stridulatory area and the density of the stridulatory teeth of the males, although females are inseparable. *G. parva* has a characteristically rectangular stridulatory area, and lacks the prominent fore wing veins of *elegans*.

Material examined

Holotype ♂, **South Africa**: Natal, Eshowe, 30.x.1980 (*Otte*) (ANS).

Paratypes. **South Africa**: 1 ♂, 1 n, same data as holotype (ANS). **Tanzania**: 1 ♂, Lake Tanganyika (*Cunnington*) (BMNH); 1 ♂, Bukoba, xii.1921 (*Miller*) (BMNH); 1 ♂, Mahagi Peninsula, Kasoge, 2550 feet, viii.–ix.1959 (*Oxford University Expedition*) (BMNH). **Zaire**: 1 ♂, Kasai, Lukenge (*Fontainas*) (MRAC); 1 ♂, Ed. Luja, Kondué (BMNH); 1 ♂, Sankuru, Beni Bendi (*Cloetens*); 1 ♂, 1 ♀, Bohor; 1 ♂, Kinshasa ('Leopoldville') (*Wilverth*); 1 ♂, Mayumbe, 3.xi.1912 (*Verschueren*) (MRAC); 1 ♂, 2 ♀, Boma, 28.iii.1913, 5.vii.1920 (*Styczynski, Schouteden*) (MRAC); 2 ♂, Kisangani ('Stanleyville'), xii.1929 (*Muller*); 1 ♂, Kisangani ('Stanleyville'), 6.vii.1932 (*Vrydagh*) (MRAC); 1 ♂, 2 ♀, 1 n, Lulua, Kapanga, iii.1933 (*Overlaet*) (1 ♂, 1 ♀, 1 n in MRAC; 1 ♀ in BMNH); 1 ♂, Haute Tshuapua, Skela, 1936 (*Buckinckx*) (MRAC); 1 ♂, Buta, 1939 (*Vanbreuseghem*) (MRAC); 1 ♂, Sankuru, Bakwanga, 5.vi.1939 (*Bequaert*) (MRAC); 1 ♂, Yangambi to Yakusu, 12.iii.1940 (MRAC); 1 ♂, Kisangani ('Stanleyville'), 5.v.1948 (ZL); 1 ♂, Tshuapua, Imbonga, xii.1952 (*Lootens*) (MRAC); 2 ♂, 1 ♀, Ubangi, Bumba, ii.–xii.1952 (*Basilewsky*) (1 ♂, 1 ♀ in MRAC; 1 ♂ in BMNH); 1 ♂, 3 ♀, Lake Tanganyika, Albertville, 14.viii.1953 (*Verbeke*) (1 ♀ in BMNH); 6 ♂, 20 ♀, Vitshumbi, i.1953, 31.iii.1953, x.1953 (*Verbeke*) (1 ♂, 4 ♀ in BMNH); 10 ♂, 31 ♀, Kasenyi, vi.1953, 11.xii.1953, 13.xii.1953, 15.xii.1953 (*Verbeke*) (3 ♂, 7 ♀ in

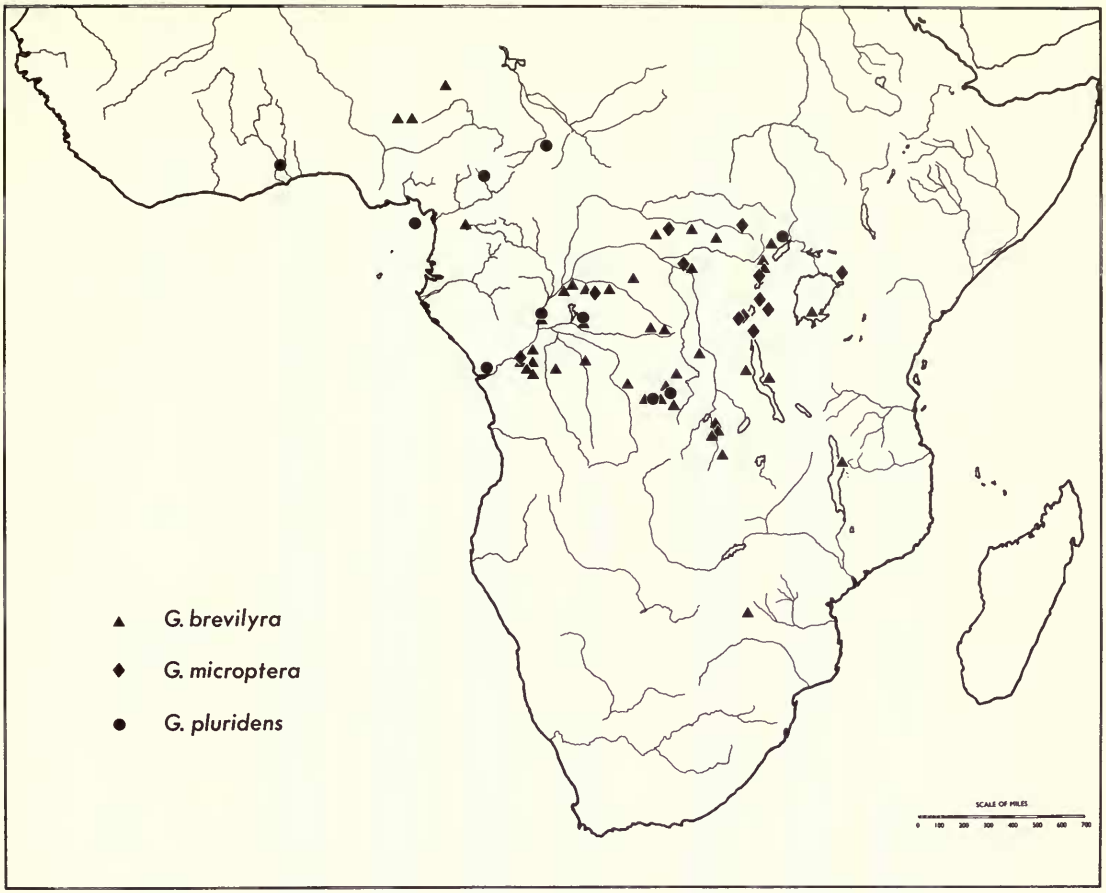


Fig. 51 Map of known distribution of *Gryllotalpa brevilyra, G. microptera* and *G. pluridens*.

BMNH); 1 ♂, Lake Albert, Ituri Sabe, 16.xii.1953 (*Verbeke*); 1 ♂, 5 ♀♀, Bezaka, 19.xii.1953 (*Verbeke*) (1 ♀ in BMNH); 2 ♂, Tshuapua Bamanya, vi.1954, iv.1961 (*Hulstaert*) (MRAC); 5 ♂, 12 ♀, Ishango, viii.1954 (*Semliki*) (1 ♂, 3 ♀ in BMNH); 4 ♂, 1 ♀, Sankuru, Djeka, 1955–1956 (*Roiseaux*) (3 ♂, 1 ♀ in MRAC; 1 ♂ in BMNH). **Somalia**: 1 ♂, Afmadu, 20–24.viii.1970 (MZSUS). **Ethiopia**: 1 ♂, Lake Hora Harsadi, Addas, c. 7000 ft, 4.xii.1926 (*Scott*) (BMNH). **Benin**: 1 ♂, 1 ♀, Cotonow (MHN). In IRSNB unless otherwise stated.

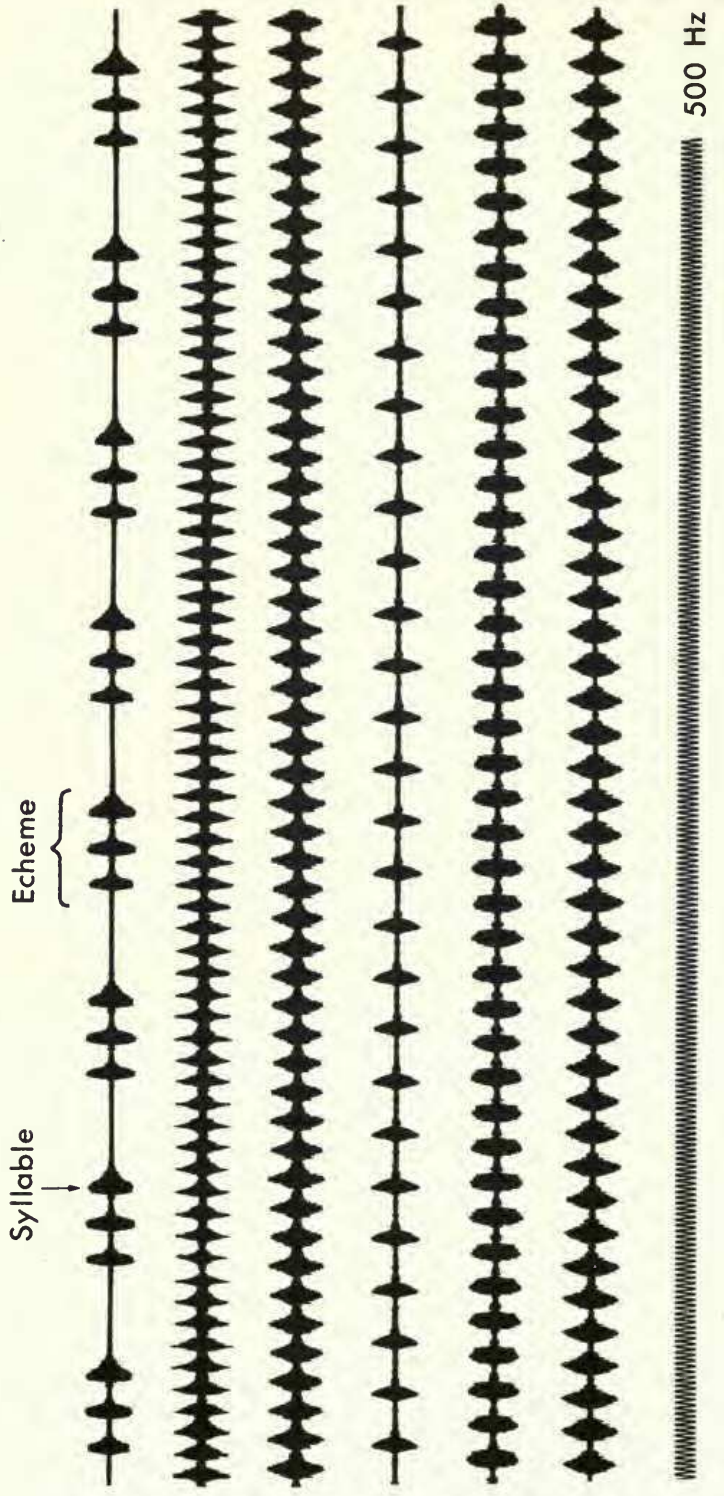
Distribution (Fig. 50). Equatorial and southern Africa, also Madagascar. *G. parva* is the only member of the *parva*-group which occurs south of the Southern Tropic.

Gryllotalpa pluridens sp. n.

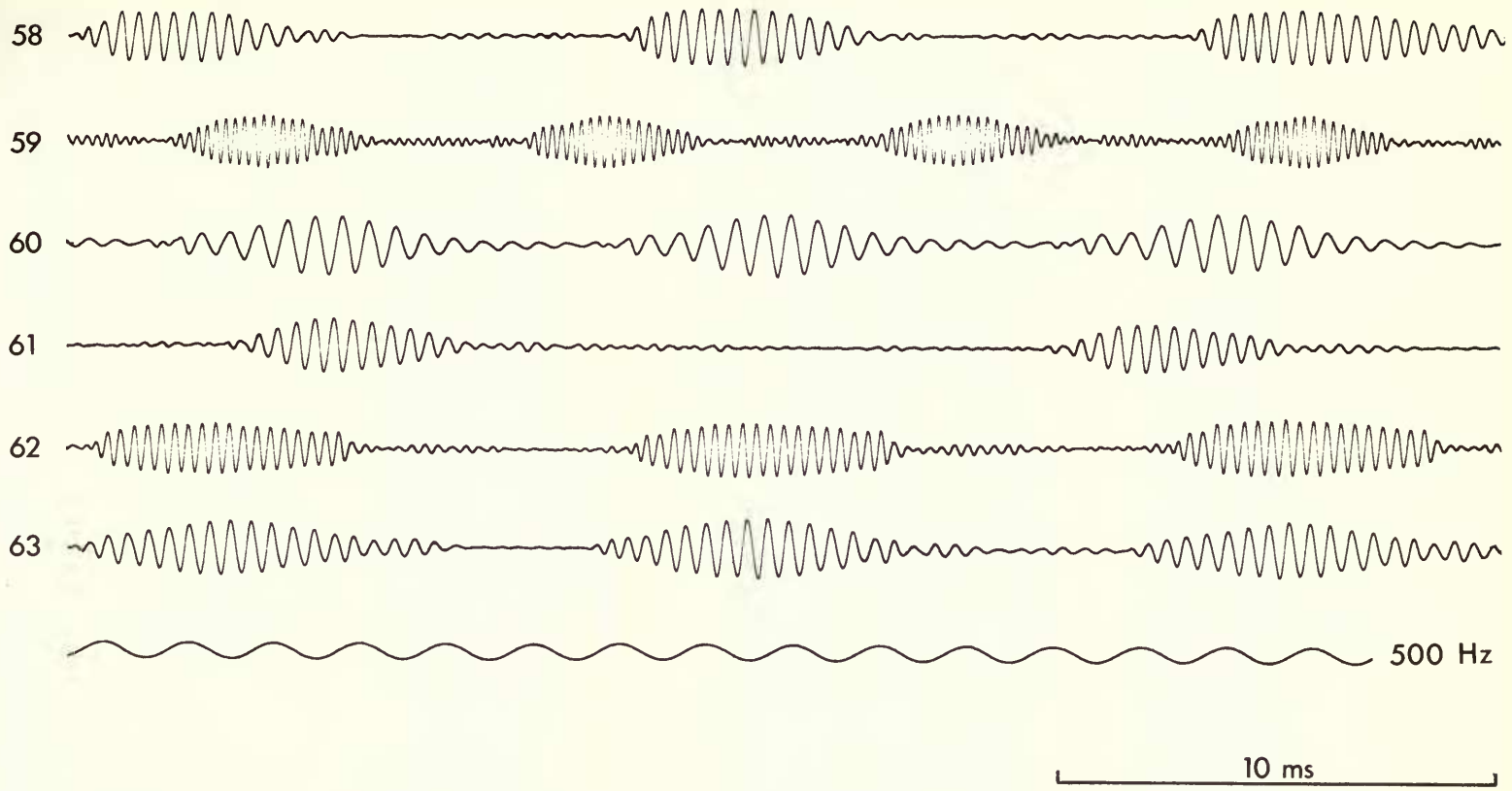
(Figs 16, 29, 42, 51)

♂. Usually fairly uniform in colour, sandy yellow to dark brown, veins of fore wings a little darker, head dark even in lighter specimens. Pronotum not unusually large compared with head. Lobes of mesonotum not exposed, concealed by pronotum and base of fore wings, never enlarged. Right fore wing as in Fig. 29; stridulatory area rather square, sometimes narrowing posteriorly; R_1 and R_s fused. Stridulatory file of right fore wing as in Fig. 16, with 76–107 teeth (mean of 23 examined: 98·0) fairly evenly spaced, 30·4–43·3 per mm (mean of 23 examined: 35·8). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 3–4 spines on internal margin. Genitalia small, with short ventral processes.

♀. Right fore wing as in Fig. 42, R_1 and R_s normally fused; if separated, then R_1 generally rather faint.



Figs 52–57 Oscillograms of the songs of (52) *Gryllotalpa rufescens*, (53) *G. bulla*, (54) *G. robusta*, (55) *G. africana*, (56) *G. parva*, (57) *G. orientalis*, showing differences in syllable repetition rate and rhythmic pattern.



Figs 58–63 Oscillograms of the songs of (58) *Gryllotalpa rufescens*, (59) *G. bulla*, (60) *G. robusta*, (61) *G. africana*, (62) *G. parva*, (63) *G. orientalis*, showing differences in carrier frequency.

MEASUREMENTS

	Males	Females
Body length	(24): 24·0–34·6, mean 28·4	(13): 21·5–32·9, mean 28·9
Median length of pronotum	(24): 7·8–10·2, mean 9·2	(13): 8·0– 9·3, mean 8·8
Length of hind femur	(23): 7·6–10·1, mean 8·8	(13): 7·9–10·3, mean 8·9
Length of fore wing	(24): 10·5–14·2, mean 12·0	(13): 10·7–13·3, mean 12·0
Length of stridulatory area	(21): 3·2– 4·4, mean 3·9	
Width of stridulatory area	(21): 2·1– 3·0, mean 2·4	
Length of stridulatory file	(23): 2·4– 3·2, mean 2·7	

DISCUSSION. The venation of the fore wing, arrangement of stridulatory teeth, and width of the stridulatory area distinguish males of *pluridens* from all other species except *spissidens*. They differ from this species principally in the overall shape of the stridulatory area, which is much squarer in *pluridens*, and in never having unusually prominent veins. Females of *pluridens* and *spissidens* are inseparable from each other, and cannot be distinguished reliably from those of the *africana*-group.

MATERIAL EXAMINED

Holotype ♂, **Chad**: Bebedjia, xi.1965 (*Schmitz*) (MRAC).

Paratypes. **Chad**: 4 ♂, 6 ♀, same data as holotype (2 ♂♂, 2 ♀♀ in BMNH); **Ghana**: 1 ♂, 3 ♀, Trans-Volta-Togoland, Kpandu, 23.xii.1959, 28.xii.1959, 3.i.1960 (*Jago*) (BMNH). **Cameroon**: 3 ♂, M'Bakaou, iii.1971 (*Chemin*) (1 in BMNH). **Zaire**: 1 ♂, Mayumbe, Luki (*Englebert*) (IRSNB); 1 ♂, Katomoja (*Lemaire*); 1 ♂, Eala, 2.ii.1923 (*Oye*) (BMNH); 1 ♂, Kibali-Ituri, Mahagi, 1934 (*Scops*); 1 ♀, Eala, xi.1934 (*Ghesquière*); 1 ♂, Lulua, Luashi, 1936 (*Faiyne*); 1 ♂, 1 ♀, Upemba N.P., Masombwe R., Kanakakazi, 1120 m, 4–16.x.1948 (*de Witte*) (♀ in BMNH); 1 ♂, Garamba N.P., Akam, 13.xii.1949 (*Demoulin*); 3 ♂, 2 ♀, Garamba N.P., 2.i.1950, 23.i.1950, 3.v.1950, 27.ix.1950 (*De Saeger, Demoulin*) (2 ♂ in BMNH); 1 ♂, 1 ♀, near Bolobo, Dwa, 1950, xii.1951 (*N'Gwe*); 1 ♂, L. Léopold II, Bokoro, 1952 (*Jans*); 1 ♂, 1 ♀, Mayumbe, T. Kipanzu, Singa to Mbomba, v.–vi.1958 (*Laurent*); 1 ♂, Mayumbe, Kitadi, viii.1958 (*Laurent*); 1 ♂, Buie, 27.iii.–5.iv.1975 (*s.b.z.*) (BMNH) **Bioko** (Fernando Poo): 1 ♂, 2 ♀ (*Nicholls*) (BMNH). In MRAC unless otherwise stated.

DISTRIBUTION (Fig. 51). Central Africa, its range overlapping that of *spissidens* from Ghana to Cameroon.

Gryllotalpa spissidens sp. n.

(Figs 17, 30, 43, 50)

♂. Fairly uniform in colour, light to dark brown, veins of fore wings a little darker. Pronotum not unusually large compared with head. Lobes of mesonotum not exposed, concealed by pronotum and base of fore wings, never enlarged. Right fore wing as in Fig. 30; stridulatory area rectangular; R_1 and R_s fused. Stridulatory file of right fore wing as in Fig. 17, with 72–96 teeth (mean of 19 examined: 85·9), fairly evenly spaced, 33·5–45·2 per mm (mean of 19 examined: 39·3). Hind wings long, extending well beyond tip of abdomen. Hind tibiae armed above with 3–4 spines on internal margin. Genitalia small, with short ventral processes.

♀. Right fore wing as in Fig. 43, R_1 and R_s normally fused; if separated, then R_1 generally rather faint.

MEASUREMENTS

	Males	Females
Body length	(19): 23·0–31·0, mean 27·8	(23): 23·6–31·8, mean 28·4
Median length of pronotum	(19): 7·6– 9·5, mean 8·6	(23): 7·0– 9·2, mean 8·3
Length of hind femur	(18): 7·2– 8·7, mean 8·2	(21): 7·5– 9·0, mean 8·2
Length of fore wing	(19): 9·2–11·8, mean 10·6	(23): 9·8–12·8, mean 11·0
Length of stridulatory area	(19): 3·4– 4·4, mean 3·9	
Width of stridulatory area	(19): 1·8– 2·2, mean 2·0	
Length of stridulatory file	(19): 1·9– 2·8, mean 2·2	

DISCUSSION. This species is very similar to *elegans*, from which it may be distinguished by its many, densely packed stridulatory teeth. Some specimens have rather prominent fore wing veins, with poorly marked cross-veins, as in *elegans*, but this feature is less pronounced in

spissidens. The distribution of *elegans* is quite different (see below). *G. spissidens* is also close to *pluridens*, differing in the shape of the stridulatory area (Figs 29, 30).

MATERIAL EXAMINED

Holotype ♂, **Cameroon**: Efulun, 10.ii.1923 (*Weber*) (ANS).

Paratypes. **Cameroon**: 1 ♂, 1 ♀, Bitye, Ja River, 3 ♂, 7 ♀, 2 n, Efulun, 25.ix.1920, 20.xi.1920, 22.xi.1920, 24.x.1922, 10.ii.1923, 10.iii.1923, 13.iii.1923, 18.iii.1923, 21.xi.1924 (*Weber*) (1 ♂, 1 ♀ in BMNH); 5 ♂, 7 ♀, Lolodorf, 2.iv.1920, 10.xii.1920, 16.ii.1921, ii.1921, 27.ix.1922, 2.ii.1923, x.1923, 2.ii.1924, 4.vii.1924, iii.1925 (*Good*) (2 ♂, 2 ♀ in BMNH); 1 ♂ (*Conrad*); 2 ♀, Harbel, 26.xii.1944, 1945–7 (*Fox, Beatty*); 1 ♂, 1 ♀, Victoria, 15.xi.1949 (*Oldroyd*) (BMNH). **Nigeria**: 1 ♂, Oban District (*Talbot*) (BMNH). **Liberia**: 1 ♂, Monrovia, 23.xi.1947 (*Olsen*) (ZL); 2 ♂, 5 ♀, Marshall Territory, 10.i.1955, 21.iv.1955, 12.v.1955, 27.v.1955, 2.xi.1955, 3.ii.1956, 7.i.1957 (*Fox*) (2 ♀ in BMNH). **Sierra Leone**: 1 ♂ (*Morgan*) (BMNH). **Guinea**: 5 ♀, near Serokoro ('Zérékoré'), 16.iii.–18.iv.1950 (*Olsen*) (4 in UZM; 1 in BMNH); 2 ♂, 8 ♀, Kindia, 1964–5 (*Dedycker*) (1 ♂, 7 ♀ in MRAC; 1 ♂, 1 ♀ in BMNH). In ANS unless otherwise stated.

DISTRIBUTION (Fig. 50). Restricted to the coastal rainforest of West Africa and the Cameroon, where it replaces *elegans*.

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Principal references are in **bold**; synonyms are in *italics*.